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The Evolution of the Mammals of the Queen Charlotte Islands, British Columbia

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THE EVOLUTION OF THE MAMMALS of the QUEEN CHARLOTTE ISLANDS, BRITISH COLUMBIA

by

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Victoria, B. C.

Province of British Columbia
Department of Recreation and Conservation

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Minister

D. B. Turner,
Deputy Minister

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COVER ILLUSTRATION - Dawson Caribou - by F. L. Beebe

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INTRODUCTION

Throughout the history of modern biology, islands have featured in the study of evolution. Both Darwin and Wallace learned much from their study of island faunas in formulating their theory of evolution by natural selection. Since this brilliant beginning, many biologists have come to realize that islands, with their simplified ecosystem and isolation from other populations in both space and time, provide natural settings for the study of numerous disciplines in relation to evolution: genetics (Ford 1955, Dobshansky 1957), ethology (Lack 1947, Bourne 1957), ecology (Anderson 1960), as well as rates of evolution (Marshall 1940, McCabe and Cowan 1945).

The Northwest Coast of North America with its remarkable number of offshore islands holds great potential for such studies. Most of the islands have appeared from under an overriding ice sheet during the last 10,000 years, so that any evolution that might have occurred on them has taken place since that time. The islands vary in size from a few acres to over a thousand square miles. As a result, the population of many small land vertebrates might vary from under a hundred, with a concomitant small gene pool, to many thousands of individuals, while the degree of isolation of a species from gene pools of the same species in other islands or on the mainland, could range from zero to almost complete. In migratory birds, for example, the degree of isolation could approach zero; in resident birds the isolation would tend to be greater. Some islands are joined to others at low tide so that passage between them would be feasible for most land vertebrates. Other islands are separated by water of greatly varying extent, depth and turbulence, these differences resulting in a considerable range of isolation for many of their inhabitants. These barriers restrict the numbers of species that can reach the islands. The size of the island also imposes limits on the number of resident species (Preston 1962). The resulting impoverished flora and fauna of the island have important effects on many of the organisms involved. Thus, members of island faunas not only live in a different genetic environment with a smaller gene pool, and restricted gene flow, but also, because of fewer competitors and predators, in a different ecological setting.

The Queen Charlotte Islands (Figure 1), are some of the most isolated islands on the Northwest Coast of North America, and therefore are of special interest in the study of the biotic evolution of this region. Thirty-four miles of Hecate Strait

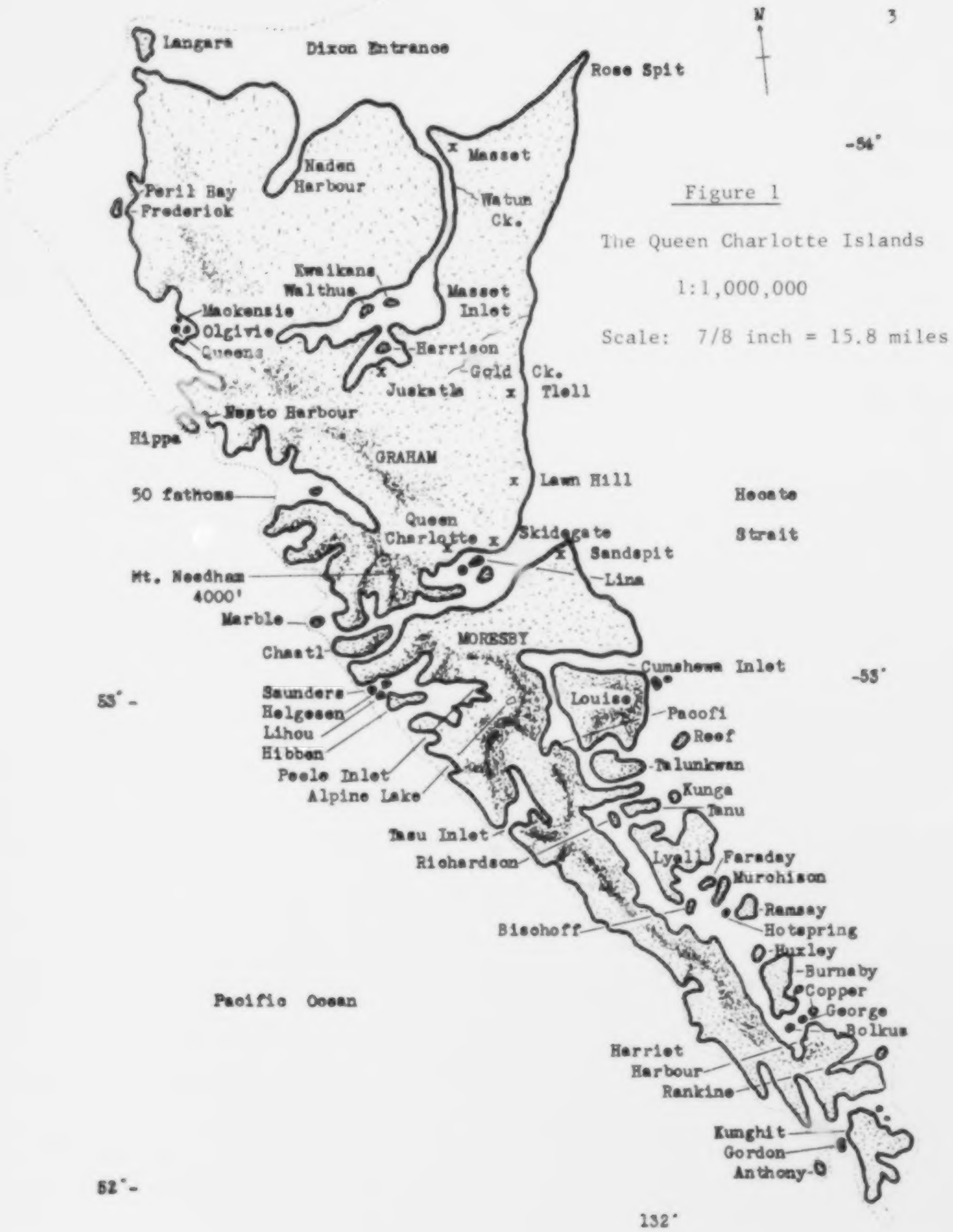

N
Langara
Dixon Entrance
Rose Spit
-54°
Masset
Naden Harbour
Peril Bay
Frederick
Watun Ck.
Kwaikans
Walthus
Masset Inlet
Mackenzie
Olgivie
Queens
Harrison
Gold Ck.
Juskatla
Tlell
Nesto Harbour
Hippa
GRAHAM
Lawn Hill
Hecate
Strait
50 fathoms
Queen Charlotte
Skidegate
Sandspit
Mt. Needham 4000'
Lina
Marble
Chaatl
MORESBY
Cumshewa Inlet
-53°
53° -
Saunders
Helgesen
Lihou
Hibben
Louise
Pacofi
Reef
Peele Inlet
Alpine Lake
Talunkwan
Kunga
Tanu
Tasu Inlet
Richardson
Lyell
Faraday
Murchison
Ramsay
Hotspring
Bischoff
Huxley
Burnaby
Copper
George
Bolkus
Pacific Ocean
Harriet Harbour
Rankine
Kunghit
Gordon
Anthony
52° -
132°

Figure 1

The Queen Charlotte Islands

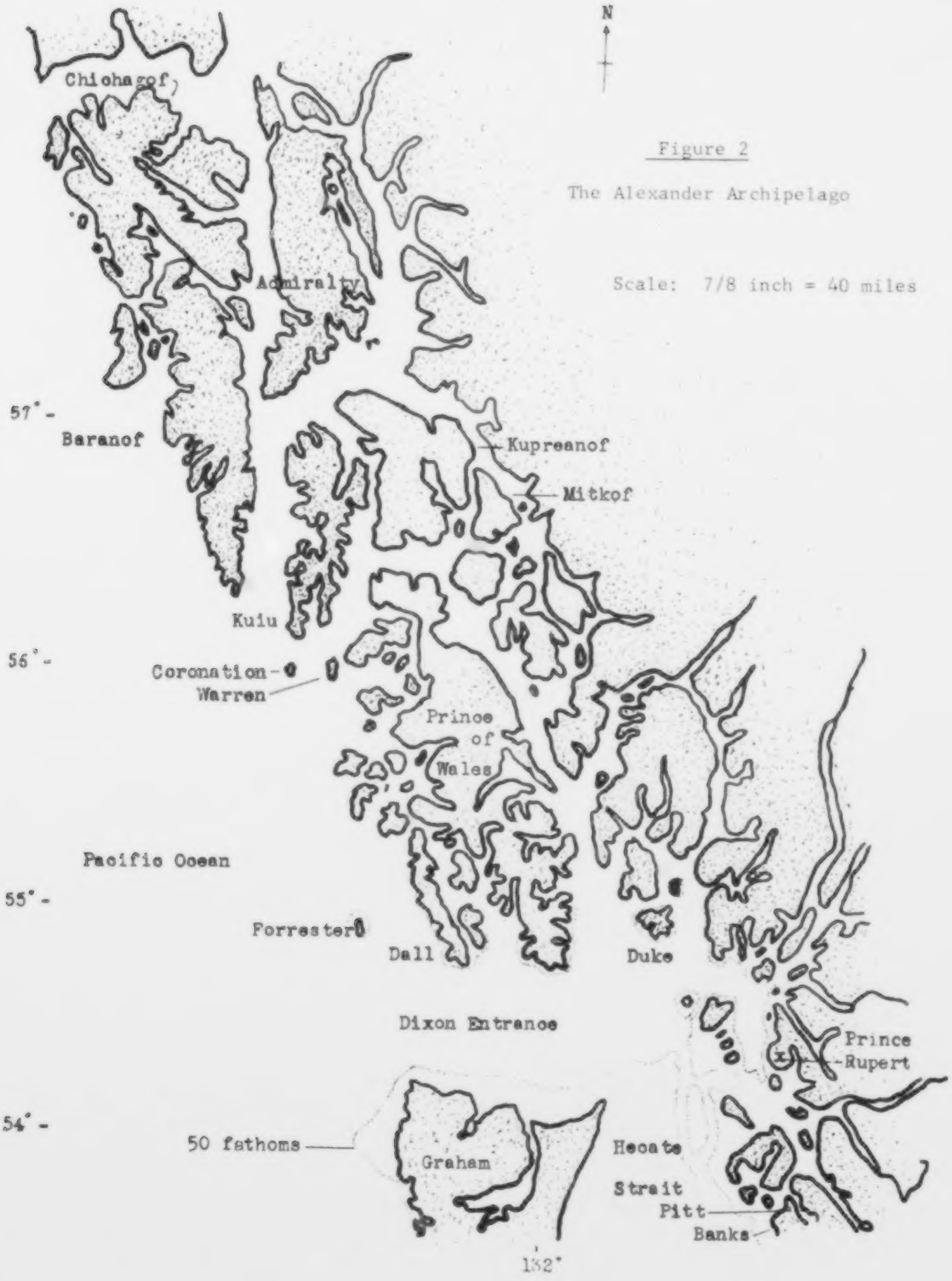
1:1,000,000

Scale: 7/8 inch = 15.8 miles

Figure 2

The Alexander Archipelago

Scale: 7/8 inch = 40 miles


N
Chichagof
Admiralty
57° -
Baranof
Kupreanof
Mitkof
Kuiu
56° -
Coronation
Warren
Prince of Wales
Pacific Ocean
55° -
Forrester
Dall
Duke
Dixon Entrance
Prince Rupert
54° -
50 fathoms
Graham
Hecate Strait
Pitt
Banks
132°

divide the Queen Charlotte Islands from the nearest mainland islands. The distance across Dixon Entrance to the Alaskan Archipelago is 31 miles, while it is 49 miles to the nearest mainland near Prince Rupert (Figure 2). The water distance is usually far greater than this and is beset by strong currents which would likely carry any waterborne waif out into the Pacific Ocean. Despite these barriers, the islands have become populated by an impoverished flora and fauna including many species, or subspecies, endemic to the islands.

These endemic forms constitute a growing list amongst the plant and animal groups. Among the former, bryophytes and alpine vascular plants are most noteworthy, while the animals include an oligochaete, an amphipod, three species of birds, and all eight species of native land mammals: a shrew, two species of deer mice, an ermine, a marten, a river otter, a black bear, and a caribou.

The absences are equally interesting. Among the mammals there are many species that now occur along the mainland coast which have not reached the islands. Other species of mammals have been introduced to the archipelago only recently by modern man and are still adjusting to their new environment.

It is the purpose of this paper to report on an analysis of the evolution of the native land mammals of the Queen Charlotte Islands, other organisms and islands being included when they contribute to the study. It is important to determine how much of the endemism present on the Queen Charlotte Islands is accounted for by reason of its being a relict population, or how much contribution is made by the insularity of the environment. If the morphological differences seen to exist between the species of the islands and the closely related ones of the mainland are of a regular nature, conforming to an obvious pattern, then it would seem that such differences are characteristic of insular faunas. Regular departures from presumed mainland ancestors have been observed in some island faunas, but at the moment there is much confusion as to their nature and extent. Hesse, Allee and Schmidt (1951) state that dwarfing of mammals and birds is a peculiarity of insular faunas. Murphy (1938) observed that many species of birds on different islands show a bill length actually greater than their presumed mainland ancestors. Zimmerman (1950) records some insular species of mammal to be larger. He reasons that this was due to the fact that a relict population of large voles (Clethrionomys)was able to exist on the outer islands, having been displaced elsewhere by a smaller form. For the same population, Cook (1961) concludes that the large size was itself a result of the insular nature of the environment. All these points of view will be dealt with in the present paper.

McCabe and Cowan (1945) state that insular isolation for a longer interval than that of postglacial time has been necessary to develop the endemic forms present in the Queen Charlotte Island fauna. They conclude that these animals have evolved on the islands from a preglacial or interglacial stock. The concept of an unglaciated area (a refugium) on the islands runs directly counter to the thinking of present day geologists (Brown and Nasmith 1962), and this subject is dealt with in condensed form in the following section.

The material for this paper has been taken from a Ph.D. thesis in which more details will be found on many points (Foster 1963).

THE SETTING

PHYSIOGRAPHY

The Queen Charlotte Islands form a scimitar shaped group, convex to the Pacific Ocean and with handle towards the south. Graham Island forms the broad northern part of the blade, whereas Moresby and many lesser islands form its tapering southern part (Figure 1).

The continental shelf that lies offshore fringing most continents is absent or very narrow off the Queen Charlotte Islands. Rugged mountains, volcanic in origin, rising to 4,000 feet and forming the westerly backbone of the islands, drop with little interruption to over 10,000 feet beneath the Pacific Ocean. The eastern side of the islands slopes gently to the shallow basin of Hecate Strait. For an account of the geology of the area see Brown (1960).

Glaciation and the problem of refugia

During the Pleistocene epoch most of Canada was repeatedly over-ridden by glaciers. The chronology of their advance and retreat is still far from reliable. Flint (1947) writes: "All we can say with confidence is that the last major glaciation has occurred within the last 30,000 years, and that on a basis of sea-floor stratigraphy the Pleistocene as a whole embraces a span of at least 300,000 years, and perhaps much more." There appear to have been four major advances on the ice in eastern North America, and at least two in the west. The last, called the Vashon in the west, is equated with the final advance in the east, the Wisconsin. Its duration is considered to have been of the order of 100,000 years.

Published geological works on the Queen Charlotte Islands are few, mostly old, and all but G. M. Dawson's (1880) refer but little to glacial features. The number and accuracy of Dawson's glacial observations is remarkable and his general outline sound, considering that the report was the fruit of only two and one half months exploring from a boat. He summarizes his observations in the following sentence (*op. cit.* p. 89B): "We find everywhere in the Queen Charlotte Islands evidence of the descent of glacier ice from the axial range of mountains toward the sea, and little or none of the passage across the group of any more ponderous ice mass."

J. D. MacKenzie (1916) of the Geological Survey of Canada studied the bedrock geology of Graham Island. His glacial observations are considered by Brown and Nasmith (1962) to be meagre and largely incorrect. Yet they are important because they have been quoted so often by biologists searching for geological evidence to support the possibility of the existence of unglaciated areas (refugia) which could have supported life during the last glaciation.

Looking east from Marble Island towards highest peaks of Graham Island. Mount Needham (about 4,000' elev.) hidden in clouds at right.

Brown (1960) reports that abundant striations in the rock illustrate how the glaciers radiated from the main axis of the islands. As they moved into Hecate Strait they must have impinged on and merged with a northward flowing mass from the Coast Mountains. The glaciers then moved out of Dixon Entrance to calve as icebergs from a great ice shelf near the continental slope. Thus a continuous mass of ice connected the Coast Mountains to those of the Queen Charlotte Islands. However, Brown and Nasmith (1962) concede the possibility of open ground on the western headlands and of nunataks. The kind of floral and faunal elements able to survive in such an environment is open to conjecture and properly the field of study of the biologist.

Dahl (1947, 1955) adds further support to the possibility of refugia on the western headlands by noting that glaciation is likely to be incomplete where high mountains abut on deep sea. Other possible refugia include beach areas uncovered by the drop in sea level during glaciation, and those areas which would have been exposed if the glaciation was not synchronous throughout the islands.

It may be concluded that the possibility of the existence of refugia on the Queen Charlotte Islands during Vashon times is certainly very real. But, as Matthews (1962) points out, the refugia would have had to exist through the entire Vashon glaciation; no minor fluctuations of the continental glaciers would have allowed populating the Queen Charlotte Islands with land mammals while glaciation was in progress. Thus the length of isolation would be in the order of 100,000 years (Flint 1947).

Looking northwest from Hotspring Island towards the main axial range of Moresby Island.

Elsewhere on the Pacific Northwest Coast there is strong evidence for the existence of refugia (Heusser 1960) from which animals and plants could have radiated following the retreat of the ice. The major refugium was south of the ice sheet in Washington. Within the area occupied by ice, the possible refugia include north-central Vancouver Island, and parts of coastal Alaska.

Refugia are unknown in the southeastern Alaska Alexander Archipelago, although parts of Baranof and Chichagof Islands are over 7000 feet and likely escaped glaciation. While there is, up to the present, no record of distinctive plants from this district, this may be due to the fact that much of it is still a virgin area for the collecting of many groups of organisms. Many of the mammals are subspecifically distinct on the Archipela Archipelago.

The largest and best known refugium of the area was in central Alaska where many large and extinct mammal species are known to have existed during glaciation (Flint 1953). Rand (1954) records others which have since extended their range, and now are found as species distinct from relatives that were in refugia farther to the south. No doubt central Alaska was a major

Looking southwest from Hotspring Island to show the rugged, dissected nature of the country.

centre of dispersal following glaciation and could conceivably have contributed to the fauna as far south as the Queen Charlotte Islands. However, this is not probably since the Islands were likely populated with mammals while more northern areas were still burdened with ice.

Eustatic Changes

Brown and Nasmith (1962) estimate that on the Queen Charlotte Islands the sea level rose to a postglacial high of about 25 feet above the present level. This conclusion was based on a study of wave-cut benches that now lie inland from the sea. A sea level rise of 25 feet would not have drowned any of the Queen Charlotte Islands examined in this study. However, in the case of Hotspring and Bischoff Island, presently the two smallest islands, the area might have been reduced beyond that minimal for some vertebrates (Wright 1931, Ford 1955, Preston 1962).

Frederick Island looking east to Graham Island showing weather-beaten Sitka spruce and rough terrain.

The greater burden of ice on the nearby mainland depressed the crust far more than on the Queen Charlotte Islands. This is judged by the wave-cut benches found four hundred to six hundred feet above present sea level (McCabe and Cowan 1945). The same authors observe that such a post-glacial submergence would have flooded many of the smaller islands along the coast.

Opinion varies on the extent of sea level depression during maximum glaciation. Brown (1960) suggests a figure of 200-300 feet; and Flint (1947) 230-330 feet. At that time all islands of the Queen Charlotte Archipelago would have been connected by land were they not covered by ice. It would then be very useful to determine the rate of wasting of the ice versus the rise in sea level as a result of world-wide melting.

Fairbridge (1960) reports that drowned beaches at the edge of continental shelves show that the maximum of glacier advance occurred 17,000 years ago, with the world-wide sea level some 300 feet lower than today. As the great North American and Scandinavian ice sheets melted, the sea level began to rise at the rate of about 40 inches per century. Radiocarbon dates for this period indicate that the rise of the sea level was not uniform but varied, with short periods of retreat. During some of these oscillations, for example, the sea level rose as much as 30 feet per century. About 6000 years ago the sea reached the present level with oscillations amounting to 10 or 12 feet since that time.

Hecate Strait is relatively shallow. For 25 miles off the northeast coast of Graham Island and to within three or four miles of the islands of the mainland's Tree Knob Group, a route can be followed where no depths greater than 72 feet are encountered (U.S.N. Hydrographic Chart, 1948 #1583). The water then deepens to about 350 feet. East of the Tree Knob Group, the mainland in the vicinity of the mouth of the Skeena River can be reached by crossing via Stephens, Porcher, and several small islands, with the widest channel only two miles from shore to shore. A sea level drop of 100 feet would bring the Queen Charlotte populations far closer to those of the mainland, and accidental transport, as on log rafts, would be far more probable.

A further likelihood is that glaciers flowing west from the mainland would have completely levelled the floor of the strait, filling in any existing channel. The present channel would have been recut by currents only when the sea level rose above it following the glaciers' melting. Thus the possibility that the entire strait stood less than 72 feet below present sea level is very real. This would have allowed the passage of organisms completely dry shod until the sea level, depressed 200-350 feet, rose to about minus 72 feet. The explanation assumes that the crust itself was stationary. But good evidence has been cited in the present report, that it was depressed at least 400 to 600 feet on the mainland. Matthews (1962) believes that the crust would have rebounded to the present level far more quickly than the sea possibly resulting in a temporary land bridge.

In summary, the evidence presented so far indicates that glacial refugia probably existed on the Queen Charlotte Islands and that a land bridge extended to the mainland at the close of glaciation. Further evidence is considered in the following sections.

VEGETATION

The luxuriant vegetation of the Northwest Coast region is nowhere more highly developed than on the Queen Charlotte Islands. In sheltered, well-drained localities where primitive conditions prevail, the forests consist of gigantic sitka spruce (*Picea sitchensis*), western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). On poorly drained sites the forest is replaced by muskeg, interspersed with dwarf lodgepole pine (*Pinus contorta*). The tree line is generally reached at an altitude of about 2000 feet with mountain hemlock (*Tsuga mertensiana*) and yellow cypress (*Chamaecyparis nootkatensis*) dominant. However, on the west coast, due to the exposure and thinness of the soil the tree line is often depressed almost to sea level. The depauperate floral nature of the islands extends to the trees themselves: there are no Douglas fir (*Pseudotsuga menziesii*), nor true fir (*Abies*), very few *Salix*, and no *Populus* on the islands.

Undergrowth under climax conditions is comparatively sparse, being composed of the ericaceous plants, *Vaccinium ovalifolium*, *V. parvifolium* and *Menziesia ferruginea*. Openings in the climax forest, formed by the space vacated by toppled trees, have been invaded by devil's club (*Oplopanax horridus*), salmonberry (*Rubus parviflorus*), and blue currant (*Ribes laxiflorum*). Fringe areas near tidewater and streams are occupied by red alder (*Alnus rubra*), willow (*Salix scoulerians*), western crab apple (*Malus fusca*), and wild currant (*Ribes bracteosum* and *R. laxiflorum*).

Moss-laden Sitka spruce forest near Masset.

The early history of the plant succession on the islands is given by Heusser (1955); the endemic plants are restricted to members of the alpine and moss flora. These topics will be dealt with in the following sections.

Masset graveyard showing mossy Sitka spruce forest.

Palaeobotany

Heusser (1955, 1960) has combined radiocarbon dating with pollen analysis of bog borings taken between Kodiak Island and northern California with the main purpose to reconstruct the postglacial plant succession and associated climatic and physiographic history. A secondary purpose was to assess the geological and zoological evidence for and against existence of refugia.

On the Queen Charlotte Islands, Heusser (1955) reports on five peat sections from muskegs on Langara, Graham and Moresby Islands. The deepest section, measuring 6.6 meters, was found on Langara Island. Broecker and Kulp (1957) place its age at 10,850 plus or minus 800 years and note that the sample should closely date the retreat of the Cordilleran ice from the ocean border. This record is older than any sections

Heusser inspected on the British Columbia and southeastern Alaskan coasts.

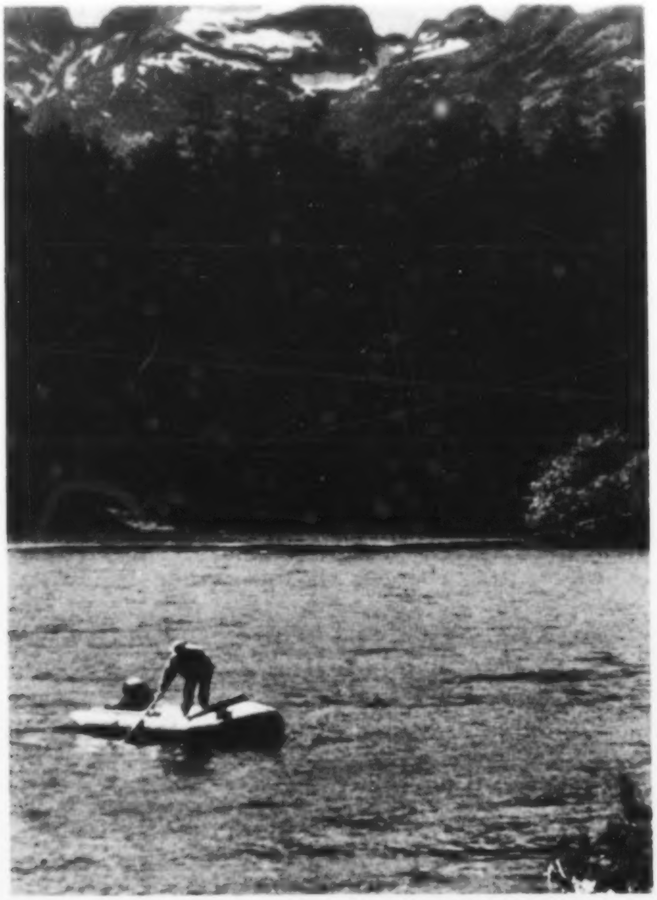
The base of the Langara record begins with a pollen assemblage indicating at least 23 species of plants. Lodgepole pine is predominant although pollen of the present climax conifers, western and mountain hemlock, and Sitka spruce represents 27% of the arboreal flora. Heusser (1955 p. 446) writes, "Such is an unexpected number of plants to find present

> at the very inception of pollen sedimentation, if it is assumed that total glaciation occurred on the Queen Charlottes. Instead of a gradual increase of species, as would be expected with a migration and succession on a deglaciated surface, the striking assemblage above is suddenly exhibited.
>
> Because the circumstances necessary for the dispersal and migration of a plant are so complex, the successful establishment of a diaspore would be highly fortuitous. The diaspore would have had to come from beyond the glacial border in Washington, 600 miles distant. It could not have come from the opposite mainland since, as will be recalled, Langara Island profiles are older than those from Ketchikan and Prince Rupert and consequently imply that plants arrived on the mainland much later owing to a lingering glacier cover. This same contention holds if it is reasoned that the base of the Langara section may have been truncated and does not begin with the earliest plant record for the locality, and further, that the numerous kinds of pollen present when peat began to form are from plants that represent the product of a long period of migration.
>
> Spruce and hemlock pollen amounting to as much as 27% of the coniferous flora in the earliest peat at Langara furnishes evidence that climax forest thrived during the period lodgepole pine was invading the deglaciated land. This information makes credible the existence of long-established forest that persisted from preglacial or interglacial time as a part of the vegetation of the nunatak complex. It further offers an explanation for the early arrival of a wide variety of pollen: plants from which this pollen was derived were associated with the above forest and other types of vegetation present in the refugia."

Vascular flora

(a) Alpine Plants

Calder (1964) estimates the total vascular flora of the islands as approximately 470 species, of which 45-65 are alpine. It is in this latter group that a high degree of endemism occurs. There are at least four unique species and five unique subspecies present. *Saxifraga taylori*, *Senecio newcombei* and *Ligusticum calderi* are very distinct. *Isopyrum savilei* is also distinct and is clearly an intermediate between a group of species restricted to California and Oregon, and another group confined to Japan. An undescribed taxon of *Geum* is either a new species



Head of Peel Inlet, Graham Island, showing dense Sitka spruce and the alpine zone.

or subspecies. Saxifraga punctata ssp. carlottae is a distinct subspecies which intergrades with other forms on the mainland. Cassiope mertensiana, Lloydia serotina, Viola biflora and Artemisia norvegica all have distinct races on the islands.

The Queen Charlotte Islands' alpine vascular flora contains close to ten per cent endemic forms making the area one of the most botanically interesting in Canada and certainly this figure is considerably higher than for any other locality in British Columbia. All the unique species appear to be confined to the Queen Charlotte Islands, except for Ligusticum calderi, which was collected by T. T. McCabe on Banks Island, immediately to the east of Hecate Strait. This species probably immigrated to Banks Island from the Queen Charlotte Islands after the Vashon ice retreat. Calder concludes that to reconcile these anomalies on the Queen Charlotte Islands with the general botanical picture in the Pacific Northwest, one cannot avoid postulating the existence of refugia on these islands.

(b) Other plants.

A startling case of disjunct distribution is found in the hymenophyllaceous fern Mecodium wrightii. It is known to occur only in Japan and on the Queen Charlotte Islands. This could be explained by assuming a continuous pan-north Pacific distribution before glaciation, and a refugium for the plant on the Queen Charlotte Islands during glaciation. It is an insignificant plant, however, and it might appear in collections elsewhere in the future. Recently, hymenophyllaceous prothallia apparently belonging to this species were found near sea level at Prince Rupert by W. B. Schofield. This suggests a postglacial immigration from the Queen Charlotte Islands or some other refugium.

Bryophytes

The Queen Charlotte Islands have been a principal centre for biological reconnaissance for many years at the expense of some other parts of British Columbia. Equal effort expended in other coastal and alpine regions might produce an equal number of interesting finds, including the extension of ranges of species presently restricted to the Queen Charlotte Islands. Nowhere is this more likely than among the bryophytes, a difficult group which is still in the early stages of exploration in the Province. Recent field work by Herman Persson and W. B. Schofield promises to alleviate the situation. Their collecting on the Queen Charlotte Islands has produced many surprising discoveries; however, final conclusions must be postponed until more collecting is undertaken in adjacent areas.

Schofield (1964) reports three endemic species on the Queen Charlotte Islands; *Campylopus* n. sp. and two others with most remarkable affinities. *Rhapidostichum* n. sp. is most closely allied to a species *R. luzonensis* which is native to the Philippines while the hepatic *Cyrtolejeunea* n. sp. has closest relatives in Brazil, Venezuela and the West Indies.

Paucity of endemic forms among this group may be interpreted as indicating a slow rate of evolution in its members. Disjunct distributions, however, are both plentiful and startling. There is a group of bryophytes, for example, *Plagiochila semidecurrens* ssp. *grossidens* and *P. rhizophora* ssp. *confusa* found only in Japan, oceanic Alaska, the Prince Rupert area and the Queen Charlotte Islands. *Takakia lepidozioides* is a subalpine species known only from Japan and the Queen Charlotte Islands. Only female plants have been discovered in both localities, and apparently it spreads by fragmenting. *Treubia nana* has the same general distribution as *Takakia.*

The Queen Charlotte Islands contain those elements which occur in western Europe, oceanic Alaska and adjacent British Columbia. These include *Marsupilla alpina*, *M. stableri*, *Gymnomitrion crenulatum*, *Anastrophyllum donianum*, *Bazzania pearsonii*, *Ditrichum zonatum* var. *scabrifolium* and *Cepholoziopsis pearsonii.*

Of this same element, but found only on the Queen Charlotte Islands and very locally in western Europe are *Leptodontium recurvifolium*, *Mastogophora woodsii* and *Zygodon gracilis*.

There is also a group of low elevation elements with strongly disjunct populations. *Anastrepta orcadensis*, *Campylopus schwartzii* and *Gehechia gigantea* have so far been found only on the Queen Charlotte Islands, Japan and in Europe. The following species are found in Alaska, the Queen Charlotte Islands and other localities listed here in parenthesis: *Pleurozia purpurea* (Europe), *Metzgeria hamata* (Japan, S. Appalachians), *Lepidozia filamentosa* (Europe, Japan). *Zygodon reinwardtii* has been recorded from the Queen Charlotte Islands, Hawaii, Alaska (one record), the Appalachians, and scattered through the tropics.

Schofield (1964) contends that the potentialities for interesting discoveries in the rich moss flora of the Queen Charlotte Islands have hardly been tapped. Serious collecting on the islands can be counted in a few dozen hours. However, even at this early stage he believes that the many anomalies present in the bryophytes on the islands can be best explained by the presence of refugia during glaciation.

OTHER ENDEMIC FORMS

In addition to the unusual plants and mammals that make their home on the Queen Charlotte Islands there is an assemblage of other organisms which is endemic to the area. These are included in this paper to emphasize the wide variety of organisms that have either evolved *in situ* on the islands as a result of isolation for a long period of time, or have been eliminated elsewhere. These conclusions are also hampered by the paucity of the collecting in adjacent areas and the complete lack of fossil evidence relating to their earlier distribution. Later an assessment is made concerning the possibility that these organisms were able to withstand the climatic conditions in the Queen Charlotte Island refugia.

Invertebrates

During two summers on the islands small collections of arachnids, millipedes, centipedes, isopods, amphipods, coleoptera, formicids, siphonaptera, hemiptera, and molluscs were made and all were submitted to experts in the respective groups. Only one form, the amphipod mentioned below, was found to be of particular interest.

Bousfield (1958) has described a new species of amphipod, *Paramoera carlottensis*, from brackish pools on the west coast of the Queen Charlotte Islands. It is morphologically closest to the group of *P. japonica*, *P. yezoensis* and *P. hayamaensis* found in the fresh-water streams of Japan.

Birds

Three subspecies of birds have been described as being restricted to the Queen Charlotte Islands: the hairy woodpecker (*Dryobates villosus picoideus* Osgood), the saw-whet owl (*Cryptoglaux acadica brooksi* Fleming), and the Steller Jay (*Cyanocitta stelleri carlottae* Osgood). A fourth subspecies, the pine grosbeak (*Pinicola enucleator carlottae* Brooks) is found on

Vancouver Island and the Queen Charlotte Islands. A fifth, the song sparrow (Melospiza melodia rufina Bonaparte) is found on the Queen Charlotte Islands and other islands to the north.

The woodpecker when compared with the mainland form is characterized by a smaller bill, very distinctive black markings on the back, and dusky sides (Osgood 1901). The saw-whet owl is slightly larger and considerably darker than nearby races (Fleming 1916). The Steller jay is also distinguished by being larger and darker (Osgood 1901). The pine grosbeak is considered by Brooks (1922) to be "quite the best differentiated of all the American forms" of the species. It is the smallest and darkest of all the races in North America. The song sparrow, according to Swarth (1923), is the darkest and largest form in the area.

From these meagre descriptions one conclusion may be drawn: all endemic subspecies of birds on the Queen Charlotte Islands are darker than their nearby relatives. This is in accord with observations elsewhere that led to the general proposal now known as Gloger's Rule.

Susan M. Smith has prepared an unpublished report on the size of the land birds of the Queen Charlotte Islands on species for which a reasonable series of specimens from both the Islands and other localities was available. Unfortunately many of her conclusions are not statistically significant because of the small number of specimens with which she dealt. Even more unfortunate is the lack of comparable material from the area directly east of the Queen Charlotte Islands; often the only specimens were from southern coastal British Columbia. Consequently some of the differences observed might reflect latitudinal change rather than insularity. Notwithstanding these and other limitations, it seems worthwhile to summarize Smith's findings.

The following 12 species were examined: hairy woodpecker, Steller jay, chestnut-backed chickadee, brown creeper, winter wren, hermit thrush, Swainson thrush, Townsend warbler, pine grosbeak, Oregon junco, fox sparrow, and song sparrow. Five measurements were made on each specimen: length of bill from nostril, length of total culmen, length of tarsus, length of tail, and length of wing. Of the 120 averages of Queen Charlotte Island samples (12 species, 5 measurements each, two sexes), 75 were larger than averages from other areas, and 43 were smaller. The greatest proportion of this discrepancy is attributable to the tarsus where 20 means averaged larger and only 4 smaller. To a lesser extent the culmen measurements tend to be larger from the Queen Charlotte Islands than elsewhere. Wing and tail measurements are about the same as in other samples. While many of these comparisons are not statistically significant, they are in line with what has been found on other islands, details of which follow in a later section.

In one species, the song sparrow, specimens from the Queen Charlotte Islands have larger averages in every measurement and in both sexes when compared with those from other areas in British Columbia. Of these 10 measurements, 6 proved to be significantly larger. For futher details on the evolution of this species in the area see Swarth (1923).

In summary, the races of birds endemic to the Charlotte area show similarities in dark plumage and sometimes longer culmen and/or tarsus. This is in accord with the literature concerning other insular birds (Murphy 1938). Whether convergent evolution or geographical relict distributions would best account for their common characteristics will be discussed in a later section.

THE IMPOVERISHED NATURE OF THE FAUNA

Islands always have a fractional sample of the organisms that live on the nearby mainland, but the reasons for the faunal hiati are often obscure or involved. In the case of the Queen Charlotte Islands there are many species not found on the islands but which occur on the mainland immediately to the east. Either the animals reached the islands and subsequently became extinct, or else the animals never did inhabit the islands. Since the geological history of pre-Vashon time in the region is obscure, I shall confine the discussion from the Vashon era to the present.

The only example of a species known to have colonized the islands and later become extinct is the Dawson caribou. There are possibly other examples but up to the present time there is no fossil evidence.

There are two main and related causes of insular extinction: either the endemic form fails to adapt to a changing habitat, or else it succumbs before a more successful competitor introduced at a later time. For example, the onset of glaciation doubtlessly forced many species into extinction. The diminishing tundra area since glaciation might have brought the caribou to the edge of extinction, while the recent introduction of the coast deer might have completed the process. However, the changing habitat on the Queen Charlotte Islands during the last 10,000 years would likely have had little affect on the vast majority of forest mammals that are now present on the nearby mainland but absent from the Queen Charlotte Islands; coast forest has persisted on the islands throughout this time and perhaps during the Vashon glaciation as well. Further, it is likely that most of the coast forest mammals and birds not present on the Islands would have found a suitable habitat there. Apparently the habitat has not been important in contributing to the impoverished nature of the vertebrate fauna.

The other major factor affecting the survival of animals on islands is that of the introduction of new species, this being closely linked, as pointed out by Preston (1962), with the area of the island concerned. For example, Main (1961) notes that two species of macropods are not found together in an insular situation unless the area is more than six square miles. The introduction of a new species into such enclosed environments may force one or more species to extinction as a result of more efficient competition, predation, etc., on the part of the newcomer. If the forms are similar, a most reasonable explanation has been put forward by Serventy (1951), who considers Gause's Law as applicable. (Gause (1934) experimentally demonstrated that two species with similar ecology cannot co-exist in the same habitat).

I consider it unlikely that the relatively great area of the Queen Charlotte Islands is presently limiting the numbers of species living there. Some individual islands are over 50 miles long. However, other islands are much smaller and on these the likelihood of the area limiting the number of species is more plausible. In the native mammals there is some evidence that smaller islands have fewer species. Marten, for example, have never been observed on any island smaller than Louise Island. But as this species is often elusive, this evidence may not be significant.

That the minimal area factor may play an important role where an introduced species is concerned is demonstrated by the case of the roof rat (Rattus rattus alexandrinus). It was introduced to the Queen Charlotte Islands many years ago, and with the aid of the commerce which was widely spread then, this species was able to reach many islands. On the two large islands (Graham and Moresby) the rats generally remain close to settlements, but on the smaller islands they become independent of man and apparently occupy the entire island.

All islands (except 'sea bird' islands) larger than 10 acres were found to have populations of *Peromyscus* except where there were rats. All islands sampled which were smaller than Lyell area and Kunghit Island area and which had populations of rats, had no populations of *Peromyscus*. Both Lyell and Kunghit Islands had the lowest density of *Peromyscus*, in fact none could be caught on Kunghit Island in the summer of 1961. Elsewhere *Peromyscus* tended to be very abundant in the trap-line catch. *Sorex* (shrews) and *Rattus* could exist together on small islands apparently because there is little interaction between them.

A third suggested reason for an animal to become extinct on an island is that if the breeding population is very small, the concomitant in-breeding may "drift" the animal to extinction (Wright 1931). This might have occurred on the smallest islands (Bischoff, Hotspring) in the case of small mammals, but not in that of the larger mammals which can likely swim from island to island and are thus potentially capable of making the whole Queen Charlotte Islands their range.

In conclusion, as a result of the large size of the Archipelago and the relative stability of the major habitats for the last 10,000 years or more, it does not seem likely that many species of animal have reached the islands in this time and since become extinct. We must then assume that the vast majority of animals not present on the Queen Charlotte Islands but present on the nearby mainland, have never reached the islands in the period being considered. Why these particular animals did not make the crossing while others did will be considered next.

In comparing the immigrants and non-immigrants, no pattern is readily discernible. For example, the terrestrial marten is present on the islands while the water-loving mink did not cross the water barrier; black bears are on the islands, but there are no grizzly bears; deer mice are present but field mice (*Microtus*). are absent; caribou (formerly) but no deer; blue grouse, but neither willow grouse nor ptarmigan; Steller jay but no Canada jay, and so on.

There are at least two possible explanations for this distribution; either the distribution is due to pure chance, or those species absent on the islands were not present on the opposite mainland when there was a comparatively easy access to the Queen Charlotte Islands.

The first Darlington (1957) terms the "sweepstake" route. It is very fortuitous for a land mammal to be on a log raft drifting towards an island. Similarly, not every species of bird would get caught up in a particular storm that is blowing from the mainland to the islands. McCabe and Cowan (1945) demonstrated the importance of log rafts which are frequently formed by slides coming down the wet, steep, mountain sides into the sea, carrying all the biota with them; however, the chances of such a raft cutting across the strong tidal currents and prevailing wind to reach the Queen Charlotte Islands is remote. On the other hand, wind storms and other chance dispersal likely have played an important part in accounting for the species of birds found on the islands. In other parts of the world such instances have been cited in the literature. Salomonsen (1951) writes of a storm blowing a breeding population of fieldfare (a thrush) from northern Scandinavia to southwest Greenland. Falla (1953) cites four examples, one of which is the most famous: in 1856 a breeding population of Zosterops was blown from Australia to New Zealand where it is now one of the commonest species.

The distribution of mammals in the region is perhaps best explained by the hypothesis that those mammals present on the Islands were either resident during glaciation or they were present on the mainland just after glaciation when a land bridge would almost certainly have existed. Those mammals not now present on the Queen Charlotte Islands on the other hand were not on the nearby mainland coast at this time.

Finally there is a distinct possibility that the Haida Indians played an important role in helping to introduce species of mammals to the Queen Charlotte Islands. One can easily imagine a small mammal being accidentally brought to the islands in the cargos and there is evidence that they brought over at least one introduction of Peromyscus (see later).

In the case of the larger mammals introduction in this manner must have been deliberate. I know of no reason why the Indian would have taken weasel, marten, otter, or caribou to the islands, but since the black bear is important in their folklore and cubs are relatively easy to secure, I think it has the best chance of being transported in such a manner. However, there is little likelihood that it will ever be proved to have occurred.

SURVIVAL IN A REFUGIUM

Having established the probability of refugia existing on the Queen Charlotte Islands during the last glaciation, it is necessary to try to assess the probability of different organisms being able to withstand the conditions one might expect in a refugium.

Palaeotemperatures for the Pleistocene, determined by Iversen (1954) and Emiliani (1955) record the minimum temperature at about 6°C below present. From what is known of plant growth and seed germination under relatively low temperature conditions , it seems unlikely that a 6° C depression would be critical to many of the plants now growing in unglaciated tracts representing probably refugia. Heusser (1960) concludes that temperature during glaciation would not have been a limiting factor for forest species on the Queen Charlotte Islands. That all endemism in the vascular plants is confined to the alpine plants is evidence that they, too, were able to withstand the climate.

Brown and Nasmith (1962) state that any unglaciated area on the Queen Charlotte Islands would have been swept by gales and snowslides. It is impossible to completely refute this comment. However, gales are of little consequence to the biota, and snowslides depend on local circumstances and cannot be thought of as major forces of exclusion.

Study of present day nunataks (Cooper 1942, Kornerup 1879, Osterfeld 1927, Heusser 1954) indicates that the inhospitable refugia envisaged to have existed on the Queen Charlotte Islands could very likely have supported plant life.

Where plants exist there are always some animals. Some species such as the caribou or marten are closely confined to a habitat type, while others, the deer mouse or cougar, for example, are not found in a single vegetation type.

On the Queen Charlotte Islands the extent of the animals' requirements would very enormously. Amphipods and oligochaetes could presumably be satisfied with small patches of suitable microhabitat, overwintering harsher times in a quiescent state. Deer mice and shrews, active the year round, would demand a larger area of suitable habitat and the opportunity of feeding during the long winter. Presumably bench areas would often have remained open, at least at low tide, and would have greatly contributed much to these small mammals' diets as, indeed, they still do.

The carnivores present on the Queen Charlotte Islands, the ermine, the marten, the river otter, and the black bear, might have eked out their existence by roaming over the glaciers from refugium to refugium, feeding on the limited vertebrate and invertebrate fauna. As with the smaller mammals, they could have gained much of their sustenance from the sea border. Marten and bear, for example, are still most commonly seen patrolling the littoral zone. Otters are usually seen feeding in the sea rather than in rivers. Of these four carnivora, the ermine has the most arctic distribution today, and likely would have experienced the least difficulty living in the refugia.

The Dawson caribou presents a different problem since all caribou herds alive today demand extensive tundra or alpine areas on which to graze. In view of the severity of the last ice age here, it seems unlikely that such a habitat would have been present in sufficient quantity on the Queen Charlotte Islands during glaciation to have supported a herd of caribou. It is possible that they also could have fed on the littoral zone plants, but this is improbable since no caribou today does this to the extent that would have been necessary on the Queen Charlotte Islands.

The endemic subspecies of birds, the saw-whet owl, hairy woodpecker, pine grosbeak, and Steller jay, are all non-migratory and cold hardy. However, they would have needed more than a forest of krummholtz trees to support their existence. That a suitable forest of sufficient size existed during glaciation cannot be proven, and on the geological evidence, it would seem unlikely. The song sparrow might have been able to sustain itself by feeding on the beach, a form of behaviour very apparent now, but whether it could have otherwise survived is a matter of conjecture.

Although earthbound organisms must have survived the entire glaciation on the Queen Charlotte Islands or become extinct by the time the glaciation ended, it is possible that storms blew birds to the islands at any time during glaciation from the Washington refugia. Members of the subspecies of birds endemic to the Queen Charlotte Islands could have populated the area as wind-blown waifs during a phase of moderate glaciation, thus alleviating the necessity of having to survive the entire Vashon ice advance. This is particularly possible for the pine grosbeak, song sparrow and Steller jay which often travel in flocks, but seems unlikely for the hairy woodpecker and saw-whet owl which are usually solitary. In a later section I shall examine the evidence that these races could have evolved as a result of isolation in postglacial times.

In conclusion, the vegetation persisting in refugia is thought to have been sufficient to have supported a limited fauna of invertebrates, shrews, mice, and mustelids. Bear might have also persisted. On the other hand, it seems most probably that the caribou and the terrestrial avifauna arrived subsequent to the close of extensive glaciation.

SUMMARY AND CONCLUSIONS

The first major section of this paper has been concerned with the Queen Charlotte Islands as a habitat for land mammals during the last 100,000 years. It is concluded, from geological, botanical, and zoological evidence, that limited refugia almost certainly existed on the Islands during the extent of the Vashon ice advance with temperature and snow conditions likely conducive to a krummholtz forest sufficient to support the life of invertebrates, and small to medium-sized mammals, but not caribou nor a permanent population of birds. The caribou and perhaps all the other mammals could have readily immigrated from across Hecate Strait when this area was dry, or almost dry, immediately following the retreat of the ice. This problem will be considered further in the next section.

A notable proportion of the lower organisms show affinities with forms living in Japan. These disjunct populations probably represent the remnants of a continuous North Pacific distribution of pre-Vashon times.

It is now necessary to examine the eight species of native mammals in turn and attempt to reconstruct their past history in the Charlotte setting. By so doing it might be possible to determine whether they owe their particular characteristics to their being relicts from a preglacial age, or to having evolved most of them as a result of lengthy isolation.

THE EVOLUTION OF THE NATIVE LAND MAMMALS

INTRODUCTION

Methods and Materials

The summers of 1960 and 1961 were spent on the Queen Charlotte Islands obtaining as large a series as possible of the native organisms, especially the native mammal fauna. The mammal collection includes some specimens collected by C. J. Guiguet of the Provincial Museum, Victoria, and I. McT. Cowan in earlier summers. Shrews (*Sorex obscurus*) and deer mice (*Peromyscus*) were the mammals most readily taken, and make up the great bulk of the specimens. These were most eagerly sought, as they are the only species to show detectable variation from island to island within the Queen Charlotte Islands.

Generally, both skins and skulls were retained, although occasionally the skull alone was kept. Some specimens were pickled entire; others had only their measurements taken (shown in parentheses in the following list). The collection includes 815 specimens (plus 321 only measured). The terminology used follows Cowan and Guiguet (1956).

153 specimens (11) of *Sorex obscurus elassodon* and *S. o. prevostensis* from 26 islands

515 (310) of the deer mice *Peromyscus maniculatus keeni* and *P. sitkensis prevostensis* from 29 islands

35 pine marten *Martes americana nesophila*

6 river otter *Lutra canadensis periclyzomae*

42 black bear *Euarctos americanus carlottae*

No specimens of the ermine *Mustela erminea haidarum* nor of the Dawson caribou *Rangifer dawsoni* were taken or seen. Of the former there are 17 specimens in existence, none in Canadian collections, and the only three specimens of the latter species are deposited in the Provincial Museum, Victoria.

The collection also includes 56 specimens of bats: *Myotis californicus caurinus*, *M. keeni keeni* and *M. lucifugus alascensis*. Examination failed to show any characteristics that separated Queen Charlotte Islands specimens of bats from those of the mainland. Considering their high mobility and therefore opportunity for gene exchange with the mainland this is hardly surprising. Inasmuch as they show no discernible peculiarities, they were not considered further.

As many islands as possible were sampled. Thirty-nine were found to contain small mammal populations. These include, from north to south, 13 on the west coast: Langara, Frederick, Olgivie, Queen's, MacKenzie, Hippa, Marble, Chaatl, Saunders, Helgesen, Hibben, Anthony, Gordon and Kunghit (formerly called Prevost); 19 on the south-east coast: Louise, Talunkwan, Reef, Kunga, Tanu, Richardson, Lyell, Bischoff, Faraday, Murchison, Hotspring, Ramsay, Huzley, Burnaby, Poole Inlet, Copper, George, Bolkus, and Rankine; 6 central islands: Kwaikans, Wathus, Harrison, Lina, Burnt and Maude; and the main islands Graham and Moresby. On another 6 islands there was no evidence of land mammals: Kingfisher Bay, Agglomerate, Skedans, Boulder, Sea Pidgeon, and Lihou. Each of these contained a population of hole-nesting alcids.

Where possible collections were made on Graham and Moresby Island directly opposite to the outlying islands from which specimens were trapped. Small mammals were taken from the following localities (north to south) on Graham Island: Merle's Point, Masset, Rose Spit, Bradlie's Ranch, Watun Creek, Port Clements, Juskatla, Peril Bay, Nesto Harbour, Gold Creek, Tlell, Lawn Hill, Skidegate and Queen Charlotte City; and from Moresby Island: Sandspit, Alliford Bay, Copper Bay, Cumshewa Inlet, Peel Inlet, Alpine Lake (2000' elevation near Peel Inlet), Pacofi Inlet, Tasu Sound, De La Beche Inlet, George Bay, Harriet Harbour and Rose Harbour (Rose Harbour is an abandoned whaling station at the north end of Kunghit Island).

Additional specimens of *Peromyscus* (302) and *Sorex* (184) from the Queen Charlotte Islands, Alaska and the adjacent mainland islands of British Columbia, have been borrowed from other collections to help fill out the study series of these species.

Definitions for measurements used were obtained from Jackson (1928) for *Sorex*, Hagmeier (1955) for *Martes* and McCabe and Cowan (1945) for *Peromyscus* and *Euarctos*.

In the following sections the mammals will be dealt with in the order of increasing number of specimens. By so doing, the complexity of the analysis will develop. An attempt will be made to ascertain whether the distinctive characteristics exhibited by the Charlotte mammals are due to their being relict populations or isolated for a long period of time. Simpson (1953, p. 303) distinguished between four kinds of relicts: numerical relicts, rare survivors of a group once abundant; phylogenetic relicts, groups evolving at exceptionally slow rates and so surviving from remote times with little change; taxonomic relicts, groups much less varied than previously; geographical relicts, groups occupying a much smaller area than their ancestors. The present paper is concerned with the last, the geographical relicts. The term "relict" is defined by the Oxford Dictionary as "a widow," while "relic" is defined as "that which is left after the loss or decay of the rest." It is clear that zoogeographers are using the meaning of the latter with the spelling of the former.

In general, this section of the study is descriptive. The broader implications of the study will be left until the final section.

Sources of Variation in Mammals

The principal sources of variation in a sample are errors of measurement, differences within populations, and differences between populations. Only the last is of taxonomic significance. For a description of errors of measurement, and differences within populations, see Foster (1963, p. 51).

Perhaps here it should be repeated that recent studies in the field of the population dynamics of small mammals indicate a source of variation that may be present within all populations. Chitty (1958), in his study of the cyclic populations of the vole *Microtus agrestis*, suggests that the genetic quality of the population changes with the different levels of the population. This could result in changes in birth rate, death rate and the size of the animal. Krebs (1962) found that in two species of lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*), the body size changed significantly with the different phases of their population cycle. Chitty and Chitty (1962) observed a peak year in numbers of *Microtus* to have adults half again as heavy as in a declining year. Other body parts could have changed proportionally or allometrically.

If this phenomenon is widespread in nature, then morphological differences that have been used to separate minor taxa, such as subspecies, could sometimes have resulted from temporary changes in the relative proportion of the genotypes in a bivalent population rather than be based upon more lasting characteristics. This would throw new light on the study of evolution itself. It is taken as a basic assumption in studies such as this that animals that are morphologically similar are phylogenetically related. (For a discussion of this assumption see Bigelow (1958) and Bader (1958).) In attempting to determine evolutionary trends and relationships between closely related groups of mammals the possibility that this phenomenon masks or magnifies the morphological differences should be considered. Unfortunately direct observation and evaluation of such changes would require many years of collecting, and consequently in a short term study such as my own, the question must remain academic. It is true that in some cases comparisons could be made between samples taken during the present study and others taken at the same localities many years ago, but any differences between them could be attributed to other causes, or if no difference is observable, this could be because the two samples were collected at the same stage of their natural variation.

Rates of Evolution

Zeuner (1950) and Rensch (1959) consider the average age of a species to be between 100,000 and one million years, and of a subspecies, 10,000 to 100,000 years. However, there are some examples which indicate that evolution sometimes occurred far more rapidly. Marshall (1940) considers the endemic races of small mammals on the islands in the Salt Lake to have evolved in less than 20,000 years; Durrant (1952) believes some of the same races to be only 2,000 years old; Lonnberg (1929) cites an example of a cottid fish which is distinct after less than 8,500 years isolation; while Doutt (1942) finds an endemic race of seal (Phoca vitulina) to have become distinct in 3,000 to 8,000 years. The Porto Santo rabbit which Charles Darwin thought had become a distinct species after only 500 years isolation, is now considered to be a race of Oryctolagus cuniculus (Rensch, op. cit.).

There are many isolated populations of the house mouse, Mus musculus, which have been spread by human agency since historic times. One famous example is that studied by Jameson (1898) on North Bull Island in Dublin Bay, where a light coloured variety has appeared in about one hundred years. Further examples have been cited by Kramer and Mertens (1938), Moreau (1930), Benick (1939), Zeuner (1950) and Rensch (1959).

Factors affecting the rate of evolution include the degree of isolation, the force of selection, the size and stability of the population and the "founder" effect. Wagner (1889) was the first to propose that evolution was not possible without isolation and the concept has since been developed by many workers. Mayr (1954) emphasizes the fact that gene flow may play an important part in limiting the opportunity of a population to adapt to local conditions and points out that an island form may differ greatly from the population living in a similar habitat on the mainland, while the latter may be indistinguishable from another mainland population living a great distance away under different ecological conditions. Gene flow could be a determining factor, inhibiting change where there is interchange between populations and allowing it where they are isolated. The work of Ford (1955) and Anderson (1960) supports this view.

The quantitative relationship of potentially reproducing immigrants to the breeding natives is, therefore, one factor determining the effect of immigration on the genetic response of a deme to a local selective factor. The larger the number of immigrants in proportion to the breeding natives the greater the tendency of the immigrants to reduce local differentiation. Both the proximity of other demes and the dispersal powers of the species will influence the magnitude of immigration.

Recently Thoday (1958), and Streams and Pimental (1961), have performed a series of experiments with Drosophila populations to test whether isolation is a prerequisite for divergence under divergent selection pressures. They found that divergence was possible despite a maximum rate of gene flow; on the other hand, selection pressure was high (90%) and would rarely be experienced in nature.

It is then clear that selection intensity is a second major factor in determining the effect of gene flow. Allee et al (1949) state "If selection pressure is greater than the dispersal and cross breeding between partially isolated populations, divergence may occur. If dispersal and cross breeding outweigh selection pressure, divergence will not occur." Mayr (1947) pointed out earlier that it has never been determined how much gene flow intense selection pressure can overcome. The experimental laboratory evidence cited above indicates that extreme selection pressure can overcome maximum rates of gene flow.

To test the effect of gene flow in nature is more difficult. Haskins and Haskins (1954) have attempted to determine whether a flow of new genes into an isolated wild population would be incorporated into that population. They introduced a "massive innoculation" of a morph of guppy (Lebistes reticulatus) into a population and considered that some of the new characters were permanently absorbed by the wild forms.

In the present study, both the selection intensity and the effect of gene flow are important. While the selection intensity would rarely, if ever, reach the level possible in the laboratory, neither would the gene flow often approach that cited by Haskins and Haskins (op. cit.). Rather a delicate balance is struck between selection and gene flow.

In addition to the usual factors which promote gene flow between groups of mammals, (mobility, hardiness, fecundity, adaptability, etc.) are those agencies which aid waif distribution. On the coast of British Columbia, log rafts (Powers 1911, McCabe and Cowan 1945) and Indians played the most important role. For a detailed discussion see Foster (1963).

The part log rafts have played in the dispersion of mammals in the coast region is uncertain. Haida Indians, however, regularly crossed to the Queen Charlotte Islands and such peregrinations between the numerous villages within the Islands would have been frequent in the past. Barbeau (1952) lists the following sites as being major villages on the Queen Charlotte Islands: Langara Island, Frederick Island, Hippa, Virago, Yan, Masset, Tow Hill, Cape Ball, Skidegate, Tsahl, New Gold Harbour, Cumshewa, Skedans, Tanu, Ninstints (Anthony Island), and Tasu. Haida villages were also common on the Alexander Archipelago. The Tsimsyan Indians dominated the mainland coast to the east of the QueenCharlotte Islands with large villages at Hartley Bay and Bella Bella.

The possibility that the Indians deliberately brought over animals has already been discussed. There is a body of evidence that they accidentally transported Peromyscus to one group of islands and of all the Charlotte mammals, the deer mice would have been most likely to have been carried in the canoes. The canoes carried more than 10 people, they were often filled with baggage and litter, including food, and were often left on the beach at night where the mice most commonly were found.

In conclusion, I believe that Indian canoes have played a more important part in transporting waifs, especially mice and perhaps shrews, than have rafts. The canoes might have contributed significantly to gene flow between the populations, and thereby affected the rate of evolution, but the rafts probably did not. However, canoe travel has ceased for almost 60 years, and therefore is of historical interest only.

The size of the population, in both space and time, may affect the rate of evolution. Kramer and Mertens (1938) and Anderson (1960) have noted that the lizards on the smallest islands are most different from their mainland ancestors. The smaller the population, the more likely that genetic drift could occur (Wright 1931), the crucial number for drift being placed from 5000 (Simpson 1953), to a "few hundred or less" (Ford 1955). Some of the populations under study are presently within this range while others would be during periods of low numbers. Great fluctuations in numbers may also increase the rate of evolution (Huxley 1942), Ford (1954, 1955). The "founder" effect (Mayr 1954, p. 178) holds that "the selective value of many genes will change drastically on the altered genetic background of a newly founded peripherally isolated population. This will lead to a rapid change of gene-frequencies simultaneously at many loci, assisted by the selective effects of the change in the physical and biotic environment of the isolated area." As it is probably that many of the islands were colonized by "founders", this phenomenon could have been operative in the evolution of the characteristics of the animals in the present study.

The size and stability of the population level, the degree of isolation, the "founder" effect, and the intensity of selection, may all be operative factors in insular conditions. It is often difficult to separate the effects of one from another. In the present study, the clearly defined endemic characters may be the consequence of either the relative completeness of isolation, or the length of time of isolation. The Queen Charlotte Islands are not only the most isolated of British Columbia islands, but they may also support the oldest fauna.

THE SPECIES

Dawson Caribou, Rangifer dawsoni Seton

The Queen Charlotte Island caribou is the most intriguing of all the native mammals occurring on the islands. It is a very distinctive form, and appears to be recently extinct. Further, the population was disjunct from other caribou by at least 150 miles. For a review of the species, see Banfield (1963), Foster (1963).

The most striking characteristics of the Dawson caribou are its small stature, imperfectly developed antlers, the absence or indistinctiveness of the usual caribou colour markings and throat mane. Its colour is uniformly dull, mouse-gray. In short, it appears to be a depauperate form of the related mainland species.

There are many examples of smaller size in island forms of ungulates (Miller 1912, Goldman 1939, Goldman and Kellogg 1940, and Hesse, Allee and Schmidt 1951). This small size is thought to be the result of lack of predators on the islands and the limited food supplies resulting in malnutrition. On the Queen Charlotte Islands the caribou would have had no wild predators and primitive Haida Indians restricted themselves to coastal activities. In addition, the forest succession since glaciation could have further limited the food supply. Coast deer (Odocoileus hemionus columbianus) introduced to the Islands at the turn of the century encountered similar problems and are now dwarf in size on some parts of the range. But the deer are now abundant, presumably because they are better suited to the environment than were the caribou.

The Dawson caribou's antlers are especially aberrant. They are small, remarkably irregular, with the brow and bez tines digitate and with few other tines. The females are apparently antlerless. It appears that the reduction in body size linked to great reduction of the entlers is an example of allometric growth. Huxley (1932) writes, (p. 207), "Differences in proportional antler size in dwarf island races of deer are probably only secondary effects of differences in absolute size and when an island race is smaller, its small size is probably due in the main to environmental stunting."

The dwarfing trend in island ungulates may be rapid as in the case of deer introduced to the Queen Charlotte Islands. It is suggested that the characteristic features shown by the Dawson caribou could have appeared in as short a period as the 10,000 years since glaciation, and without the necessity of postulating isolation of the island caribou for the whole period of the Vashon advance (100,000 years). The meagre evidence at our disposal indicates that the refugia on the Queen Charlotte Islands were unlikely to have offered suitable caribou habitat. Precipitous nunataks and steep western headlands are not the habitats of the caribou, but fringe refugia on the west coast might have harboured the animal. Certainly the caribou is well suited to the climate which would have prevailed. While the problem will perhaps never be solved, I suggest that the following most likely occurred.

During the Vashon glaciation, caribou were present south of the ice sheet in Washington (Flint 1947) and in the Alaska refugium (Frick 1937, Geist 1953). One might imagine that the Queen Charlotte Islands population, lying approximately between the two, could have been derived from either source. Banfield (1961), however, considers the Dawson caribou to be clearly derived from a southern forest caribou, such as R. tarandus fricki. This is to be expected since the glaciers would have begun their retreat in the south, and it seems most likely that the caribou would have moved northwards, closely following the retreat of the ice. They apparently by-passed Vancouver Island as there is no evidence that they ever existed there. By following the coast the caribou would have come to the areas first to become ice free. They crossed over to the Queen Charlotte Islands either on the ice, or on land, or perhaps by swimming a short distance. Here they became isolated as the sea level rose to cover Hecate Strait, and whereas the mainland caribou continued to spread north and east, finally forsaking the westerly slopes of the coast range which they found unsuitable, the Dawson caribou were stranded in the Coast Range environment and apparently suffered in stature and viability as a result. As the wet forest closed in upon them, they were unable to hold their own. Centuries of inbreeding among the small herds perhaps contributed to their decline. Finally, at the turn of the last century, the successful and versatile coast deer was introduced, and it rapidly multiplied and spread throughout the islands. The heavy grazing and browsing quickly affected the habitat. This might have proved to be the final blow to the caribou.

Caribou failed to populate the mainland islands, either because they were covered by ice when the animal crossed to the Queen Charlotte Islands, or because they were still below sea level at that time. Alternatively, the changing habitat and early natural introduction of the deer to these islands could have eliminated the caribou for the reasons detailed above.

River Otter, *Lutra canadensis periclyzomae* Elliot

This species has become completely adapted to living in the marine environment of the Pacific Coast. Although usually secretive, abundant slides, dung, and other signs, show it to be fairly common along most of the coast. In spite of this, otter are generally scarce in collections. All species except *Lutra mira* from Prince of Wales Island, southeastern Alaska, have become synonyms of *L. canadensis*, and Hall and Kelson (1959) believe its synonymy will be assured when more specimens are taken. One species (*L. vancouverensis*) has disappeared into synonymy by first becoming *L. c. vancouverensis* (Dalquest 1948) and finally synonymous with *L. c. pacifica* (Cowan and Guiguet 1956).

In such a plastic species, whose members show marked variation according to age and sex, a substantial series of specimens is essential to reach any conclusions about the evolutionary processes that have occurred within the group. This series still lacking, however, it is clear that *periclyzomae* is a poorly differentiated race (Foster 1963).

During the Vashon glaciation, it is likely that all river otter were in the area south of the continental ice sheet; the refugia on the Queen Charlotte Islands would not be very suitable for this species since rivers would have been frozen much of the year. True, the species might have persisted on the parts of the west coast of the islands that were open, but the absence of striking differentiating characters in the Charlotte population mitigates the necessity for a lengthy period of isolation in a refugium.

At the close of glaciation the otter would have been quick to advance north with the retreat of the ice. It could have crossed to the Queen Charlotte Islands on the ice, on land, or by swimming. The species finally made its way north to the Bering Sea and east beyond Hudson Bay. The population on the Queen Charlotte Islands became somewhat isolated from that of the Alaskan Archipelago and the mainland as the sea level rose to widen the water gap. This may not have been an effective barrier since there is evidence that river otter can swim considerable distances across the open sea. Cowan and Guiguet (1956) report that a semi-tame pair was taken from the Victoria harbour to the Stanley Park Zoo in Vancouver and later escaped. In three weeks both were back in their old haunts in Victoria. The minimum distance involved is 70 miles with a minimum water crossing of 15 miles.

In view of the doubtful discriminating morphological characters separating the race from neighbouring races, it seems very plausible that gene flow between the Queen Charlotte Island otter and the mainland populations is continuing to the present day.

The Short-Tailed Weasel or Ermine, Mustela erminea haidarum (Preble)

During 8 months on the islands we saw no trace of this species. The local people observed that ermine were generally very scarce and only one trapper, George Sahenovitch, claimed that he had recently seen one. The present study, therefore, is based on animals collected earlier.

Originally the Haida weasel was described as a distinct species, Putorius haidarum by Preble in 1898, but since then it has been reduced to subspecific level by Hall (1944). The entire collection of this race, amounting to 17 specimens, has recently been examined by Hall (1951) in his monograph on the American weasels. He notes that haidarum differs from richardsoni, present on the adjacent mainland and east to the Atlantic Ocean, in having the skull of the male actually larger in its anterior part (breadth of rostrum, interorbital breadth and orbitonasal length) but with measurements of other parts somewhat less. In relation to the basilar length, the tympanic bulla is shorter but all other measurements are greater. In the skull of the female, the width of the tympanic bulla and anteroposterior extent of the inner lobe of the first molar are the same; in all other measurements the female of haidarum is larger, and in relation to the basilar length, all measurements are greater except the depth of the skull at the anterior margin of the basioccipital, and the width of the tympanic bulla, which are less.

Hall (1951) writes that it is clear that the skull of haidarum tends to be larger than fallenda (Vancouver area) anguinae (Vancouver Island) and alascensis (mainland of the panhandle of Alaska) but smaller than nearby races from the Alaskan Archipelago (celenda, seclusa). In every case the island form is found to be larger in most skull characters than the nearest mainland race. In haidarum this is most noticeable in the front parts of the skull including the teeth.

As is usual in the mustelids, the male on the average is larger than the female. Hall (*op. cit.*) notes that the skull of the female *richardsoni* averages 52% lighter than the male. As may be seen from Figure 3, all mainland ermine for which there were sufficient specimens show that same trend; the skull of the female is at least 42% lighter than that of the male. However, in *haidarum* the skull of the male is 25% lighter and the skull of the female 24% heavier than in *richardsoni*. This, of course, has the effect of bringing the weights of the two sexes much closer together in *haidarum*; the female averaging only 29% lighter than the male.

While Hall (*op. cit.*) failed to point out the relative lack in sexual dimorphism in *haidarum*, he did note it for the race *anguinae* from Vancouver Island where it is even more apparent, with the female only 25% lighter than the male. This is the lowest disparity between the two sexes for any North American subspecies of ermine.

Unfortunately, the four races of ermine from the Alaskan Archipelago are poorly represented in collections and it is as yet impossible to determine whether all ermine tend to show less size difference between the sexes on islands. The two examples cited in the present study are certainly suggestive.

Hall (*op. cit.*) concludes:

> "*M. e. haidarum* has more claim to full specific status than any other race of ermine because the diagnostic structural features are numerous and individually of relatively great degree. Indeed, individual variation appears not to bridge the gap between any population of *haidarum* and other subspecies and strong reasons could be advanced for according *haidarum* the status of a full species. It differs from the subspecies of *erminea* on the ajoining mainland and the adjoining islands to the north and south and agrees with the Arctic races (*arctica*, *polaris*, *semplei* and *kadiacensis*) in great extent of the colour of the underparts, extension of this colour onto the underneath side of the tail, long black tip of the tail and general form of the skull including the relatively heavy preorbital region. The colour, although darker than the Arctic subspecies, is lighter than in the insular races immediately to the north and south. In combination, the features mentioned could be taken as indication that *haidarum* is a relict population from a former glacial period. Assuming that it is a relict population, the colour may have become slightly darker since that period, but the main response appears to have been a decrease in size for this is

> a much smaller animal than the Arctic ermines. The size is about what would be expected if one were to judge by the slightly larger ermines on the islands of southeastern Alaska to the north and the smaller ermine on Vancouver Island to the south. This would be predicted in Bergmann's Rule.
>
> "The ermines of the islands of southeastern Alaska, excepting possibly the incompletely known *seclusa*, have fewer characters of the Arctic races and more characters of the races of the adjoining mainland. Therefore, a possible inference is that the distinctive characters of ermines of the Alaskan islands developed with the aid of isolation from stocks which reached the islands after the glacial period. *M. e. haidarum* may have found its way to the Queen Charlotte Islands in the glacial period."

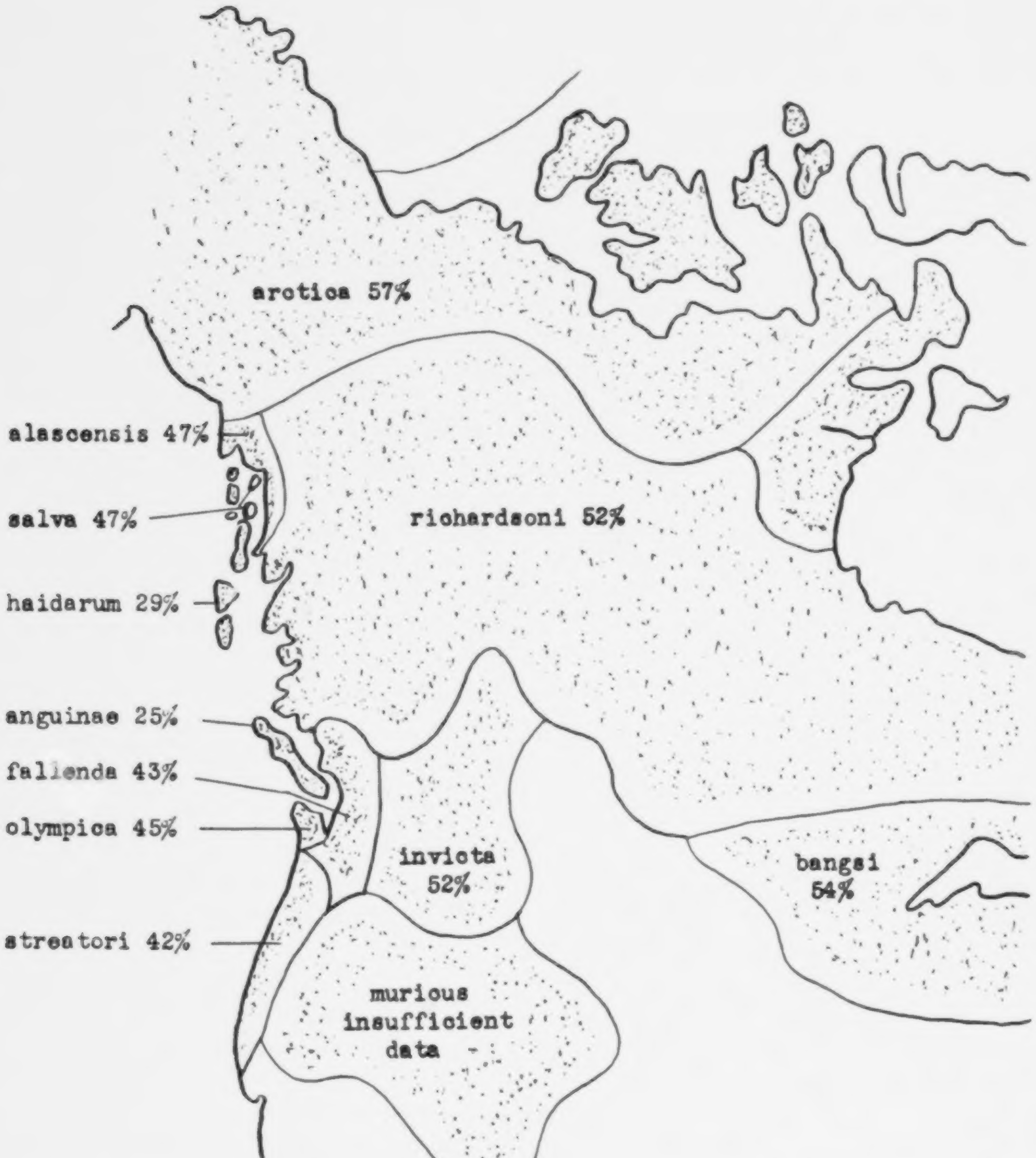
While Hall does not point out which glacial period he means, I assume he is referring to the last, the Vashon. Also, as pointed out earlier, it is unlikely that animals would have found their way to the Queen Charlotte Islands "in (= during) the glacial period" but rather only between them, in this case, before the onset of the Vashon ice advance.

The ermine ranges the entire arctic and consequently seems most admirably suited for life in a glacial refugium. It is a highly mobile animal and could have circulated from refugium to refugium on the islands searching for food. Preble (1901) finds the shorelines the best areas to trap this species and this might indicate a propensity for littoral feeding during glacial times.

It is difficult to explain the scarcity of this subspecies over at least the last twenty years, since shoreline food, if taken, would always be available. Small birds also are generally plentiful and, in the last few years, deer mice have been abundant.

In conclusion, it appears that at the onset of the Vashon glaciation ermine were confined to the Alaska, Queen Charlotte Islands, and main continental refugia. As the ice retreated, Alaska ermine spread eastward across the Arctic to Greenland, continental ermine, characterized by *M. e. richardsoni*, moved north to the treeline and west as far as the Alaskan Archipelago, while *M. e. haidarum* remained on the Queen Charlotte Islands. Since *haidarum* is a well characterized race this suggests that few, if any, ermine crossed to the Queen Charlotte Islands at the

Figure 3: Skulls of some North American ermine; mean weight of the males expressed as a percentage increase of the mean weight of the females. Compiled from Hall 1951.


arctica 57%
alascensis 47%
salva 47%
richardsoni 52%
haidarum 29%
anguinae 25%
fallenda 43%
olympica 45%
invicta 52%
bangsi 54%
streatori 42%
muricus insufficient data

close of glaciation. Mainland weasels, like many of the other species of land mammals absent on the Queen Charlotte Islands, were apparently not yet resident on the mainland when the land-ice bridge was available. Whether *haidarum* is directly related to the arctic weasels, or has evolved similarly as a result of living in a like environment (the refugia) for a long time, is a moot point.

Pine Marten, *Martes americana nesophila* (Osgood)

This large, light coloured race of marten is one of the most distinctive in North America. Osgood (1901) originally described the race as a species from skulls from the Queen Charlotte Islands. For a recent review of the genus see Hagmeier (1955, 1961). Hagmeier (1955) notes that *nesophila* is almost the largest race of North American marten, with most dimensions greater than in the mainland form (*M. a. caurina*). At the 95% level of significance, and with a sample of 16 males and 17 females, he finds the following skull measurements greater than those from the nearby mainland: condylobasal length, rostral width, canine width at base, upper molar width, height of skull at bulla, length of last upper premolar, and narrowest palate width. Twelve skulls from the Alexander Archipelago are not significantly different from this series.

Hagmeier (1955) believes that at the close of the Vashon glaciation marten were present in all the major refugia. The *americana* group of subspecies existed in the refugium of the south-eastern United States, and perhaps in the Alaska-Yukon and a Rocky Mountain refugia. The *caurina* group was present in the Pacific Coastal refugium, with the Queen Charlotte Island morph (*nesophila*) in the Charlotte refugium. At the close of glaciation, *nesophila* emigrated north to the Alexander Archipelago, where some of its more extreme size characters became somewhat diluted as a result of contact with the marten which had reached the mainland coast from other refugia.

Hagmeier's evidence for the existence of marten on the Queen Charlotte Islands during the Vashon glaciation rests primarily upon the botanical evidence outlined earlier. He accepts as a basic dictum that the history of the vegetation in which an organism lives reflects the history of the organism itself. While this would be less valid for some organisms than others, Hagmeier believes that it is particularly applicable to marten, since its distribution is so closely tied to the distribution of the boreal forest. In the present case it is not conceded that the vegetation in the refugia on the Queen Charlotte Islands would have been so advanced that it contained a sizeable boreal forest of the type in which one usually expects to find marten; rather it is suggested that nesophila's ability to gain much of its sustenance from the littoral zone might have been of great significance.

Hagmeier (op. cit.) uses other evidence to support his thesis that marten survived in the Charlotte refugia, including the fact that nesophila is the most distinctive race of all North American marten, and that a time greater than post-glacial isolation would have been needed to allow the formation of such a race. This hypothesis has already been stated by McCabe and Cowan (1945). However, as pointed out earlier, it is not possible to directly equate degree of morphological divergence with the length of time of isolation, since there is too much variation between groups. Nevertheless, the fact that nesophila is highly distinctive within the species N. americana, seems to lend significance to the hypothesis.

The major features which distinguish nesophila from other marten in western North America include the large size of the skull and the pale colour of the pelage. Hagmeier (1961) indicates the clinal nature of the condylobasal length of the skull for western North American marten. In general the cline follows Bergmann's rule, with the smallest lengths in the south-western States and the largest in the Northwest Territories. The population which is most in conflict with this trend is that on the Queen Charlotte Islands. Their condylobasal lengths are larger than in populations to the north as well as to the east and south, while many of the skull measurements of nesophila are significantly larger than those seen in the nearby mainland races.

In attempting to determine the factors responsible for the appearance of the large Queen Charlotte Island form, a question of fundamental importance is posed. Is the population a relict or did divergence from mainland stock occur only after insular isolation was established? The background to this problem has already been outlined.

The following alternatives are most plausible:

A. No marten existed in the Queen Charlotte Island refugia.

1. It is possible that the northern members of the population in the Washington refugium were large (similar to nesophila), perhaps as a result of adaptations to the cold climate,

and were the leading invaders of previously glaciated areas as the glaciers retreated northwards. In this argument it is assumed that they were the invaders of the Queen Charlotte Islands, at a time when the islands were still joined to the mainland. The large marten contined to follow the retreating glaciers northwards until they reached their distributional limit at the present treeline. The sea level then rose and left the Queen Charlotte Island marten as a relict of a population of large marten. On this theory marten distinctly smaller than nesophila arrived in the general area only after the Queen Charlotte Islands had become isolated.

Had large marten followed the northward retreat of the glaciers to populate the Queen Charlotte Islands, one would still have to explain why the nearby mainland marten are small. Did a small form displace the larger one on the mainland, or did selection, favouring small individuals in the coastal mainland population, bring about the change? It would be surprising if the Queen Charlotte Island population was the only one formed in this way since there are many isolated islands in the area which could have provided refuge, however, McCabe and Cowan (1945) find no evidence of any marten on 36 coastal islands east of the Queen Charlotte Islands. It might be suggested that the coastal islands are too small to support a population of marten; however, Porcher, Pitt, Banks, Aristazabal, Princess Royal, Swindle, King and Calvert Islands are all larger than Louise Island from which marten have been taken. It is difficult to imagine marten being able to reach the Queen Charlotte Islands after glaciation without colonizing some of the far more accessible coastal islands. This I suggest is the strongest evidence that marten existed in the Queen Charlotte Island refugia during glaciation, and that the marten now resident on the mainland coast, reached this area after the sea level rose.

2. Another possible explanation is that marten of small size spread northwards from Washington at the close of glaciation and became isolated on the Queen Charlotte Islands. They then became larger on the northern mainland, perhaps due to selection for large size in a cold environment, and became large on the Queen Charlotte Islands as a result of selection, in a situation in which gene flow from the mainland was negligible. Isolation, then, is the important factor in this argument for the creation of large size in nesophila.

While this explanation would answer the problem of small marten on the coastal mainland better, it still fails to explain the lack of marten on the coastal islands, and hence it must be discarded.

Finally, both hypotheses assume that 10,000 years since glaciation would have been sufficient for such a distinct form to be produced. The general problem of rates of speciation has been discussed earlier; specifically McCabe and Cowan (1945) and Hagmeier (1955) believe that more than 10,000 years would have been necessary to have fostered such bold characteristics.

B. Marten survived in the Queen Charlotte Island refugia.

1. Before the Vashon glaciation commenced, marten were no doubt as widely distributed as they are now. It is possible that the west coast of North America, including the Queen Charlotte Islands, was populated with a form similar to nesophila, in which case the present nesophila would constitute a geographical relict population.

Unfortunately the type of fossil evidence available to Hinton (1926) in his study of Clethrionomys speciation in Europe, is not available for Martes from glaciated North America and while nesophila might be a relict of a formerly widely distributed race, it will probably never be possible to verify this.

2. The pre-Vashon population on the Queen Charlotte Islands might have been composed of average-size marten which became larger during, and because of, their residence in the refugia. The process would have been aided by the smallness of the gene pool and its isolation from other gene pools for thousands of years.

This explanation seems to be the most plausible since it is extremely likely that complete isolation, for so long would have produced some differences between mainland and Queen Charlotte Island populations. Unlike the previous hypothesis it is not based upon an unsubstantiated assumption, viz., that nesophila was once widely distributed.

Whether genetic drift or selection played the more important part is impossible to say with certainty. It is possible, as Dobzhansky and Pavlovsky (1957) have suggested, that drift and selection have interacted in determining the evolutionary changes, selection operating on materials originally determined by drift. A "few hundred or less" individuals was stipulated by Ford (1955) as being a maximum allowable for drift to occur, and it would seem likely that such numerical limitations may have been present in the island population in the refugia on the Queen Charlotte Islands for thousands of years.

If selection has played the important role in determining the large size of *nesophila*, then presumably the larger individuals have an advantage over the smaller. Rensch (1959) has given a good outline of where the advantages of large size might lie, and these reasons will be fully discussed in the final section. In the case of *nesophila*, adaptation to the cold environment present in the refugia might have been the most important single factor. At present, members of this subspecies are almost as large as those living in subarctic conditions.

The skull of *nesophila* is most distinctive in its thick heavy rostrum, and heavier dentition, especially the molars. Five of the eighteen marten stomachs examined contained parts of crabs and it is suggested that perhaps the heavier dentition and associated areas in the skull are adaptations to a change in diet from small birds and mammals to feeding upon intertidal animals.

The pale colour of the pelage of *nesophila*, in contrast to the darker pelage of forms along the mainland coast, is harder to explain. For mainland marten as far east as the Atlantic Ocean, Hagmeier (1955) finds a correlation between dark pelage and heavy precipitation, as implied by Gloger' s Rule. He neglects to explain why, however, *nesophila* should have pale pelage in an exceedingly moist environment. Up to the present no explanation for this phenomenon can be given.

In summary, the evidence that *nesophila* was resident in the Queen Charlotte Island refugia for the duration of the Vashon glaciation is strong. It is most likely that the animals evolved their unique characteristics during this long tenure.

Black Bear, *Euarctos americanus carlottae* (Osgood)

This race of black bear was originally described as a distinct species by Osgood in 1901 and is confined to the Queen Charlotte Islands. Osgood describes it as "Size slightly greater than *Ursus americanus* (read *Euarctos americanus*, specimens from Alaska to Idaho); skull more elongate; rostrum relatively more slender ; cranium less arched; teeth larger and heavier, particularly last molars; last upper molar with posterior "heel" quite elongate." This insular race lacks the brown colour phase.

E. a. vancouveri from Vancouver Island is similar to *carlottae* in having a massive skull and in the absence of the brown colour phase, but is readily distinguished from it by having smaller molars (Hall 1928). *E. a. altifrontalis* of the lower, coastal, mainland of British Columbia is described as having a more prominent "forehead" and wider molar teeth than nearby races (Elliot 1903); also, the brown phase is occasionally found. *E. a. kermodei* occurs immediately east of the Queen Charlotte Islands. The two skulls in our collections show great individual variation, "one with a short thick rostrum and a high frontal region resembling *altifrontalis*, the other with a long, narrow skull" (Cowan and Guiguet 1956). The occurence of a white colour phase in this population prompted its description as a distinct subspecies. *E. a. pugnax* ranges the Alexander Archipelago immediately north of the range of *carlottae* and is distinguished from it by its flat, depressed forehead and short and broad rather than elongate skull. Members of this race on the Archipelago apparently lack the brown phase (Swarth 1911), though it is present in about a third of the members on the adjacent mainland.

During our summers on the Islands we took every opportunity to increase the sample size of this species and the collection now comprises 32 skulls, while the list of measured skulls is increased to 42 by Osgood (1901) and Hall (1928). The skulls have been broken into three different age groups. There are 18 immature (sutures open, sagittal crest small), 16 adult (sutures mostly closed, sagittal crest large, teeth not badly worn), and 8 old adult (teeth badly worn).

For comparison examinations have been made of 14 *vancouveri* (7, 5, 2, respectively), 13 *altifrontalis* (6, 5, 2, respectively) and 11 *pugnax* (7, 5, 0, respectively). Some skulls were defective and since this made the sample sizes small, all ages were combined except those from Queen Charlotte Islands in which immature skulls were kept separate from the others.

The most useful measurement was found to be that of the length of the last molar since its length it not age-dependant. An analysis of variance on the five samples indicates that there is a significant difference (95% level) between them (F = 5.14), hence a Duncan Multiple Range Test (Duncan 1955) is applied to see where the difference lies. At the 95% level of significance, there is no difference in molar length between the samples of *pugnax*, *vancouveri* and *altifrontalis* and the two samples of *carlottae* are not significantly different from one another.

However, both samples of *carlottae* are significantly different from the other three races.

It may be assuming too much to attempt to draw inferences of the past history of the bears in the region from only one character, but until more specimens are obtained from areas adjacent to the Queen Charlotte Islands, there is no other alternative.

From the analysis of the length of the last molar of the four races, it appears that *carlottae* is more different from the other three races than they are from one another. The differences could be the result of the environment affecting the soma of the individual directly, but the fact that *carlottae* and *pugnax* appear to live in closely similar environments makes this conclusion unlikely. If the difference is genetic, the same reason invalidates evoking the explanation that it is because of different environments. More satisfactory explanations are that *carlottae* is unique either because it is more completely isolated, or because it has been isolated for a longer time than has either *pugnax* or *vancouveri*. However, since bears are seen swimming infrequently between islands and since Indians are unlikely to transport cubs to an island which already has the species, and because log rafts are not likely to carry off an animal as large as a bear, it appears that *pugnax* is almost as well isolated as *carlottae*. The most plausible explanation is that the latter lived in the Charlotte refugia and developed its large molars during the lengthy isolation there. Perhaps the heavy molars are an adaptation to the coarse beach food (crabs, etc.), which the bears might have been forced to rely heavily upon during the glaciation.

In summary, because of the smallness of the samples from areas adjacent to the Queen Charlotte Islands and since the skull varied both in size and proportion with age, only a gross evaluation of the recent evolutionary history of this species is attempted. The length of the molar indicates that in this measurement *carlottae* is more different from *pugnax*, *altifrontalis* and *vancouveri* than these three are from one another. The explanation proposed for this phenomenon is that *carlottae* lived in the refugia on the Queen Charlotte Islands during the last glaciation and therein developed its distinctions.

All the insular bears studied lack the brown phase; the reason for this is unknown.

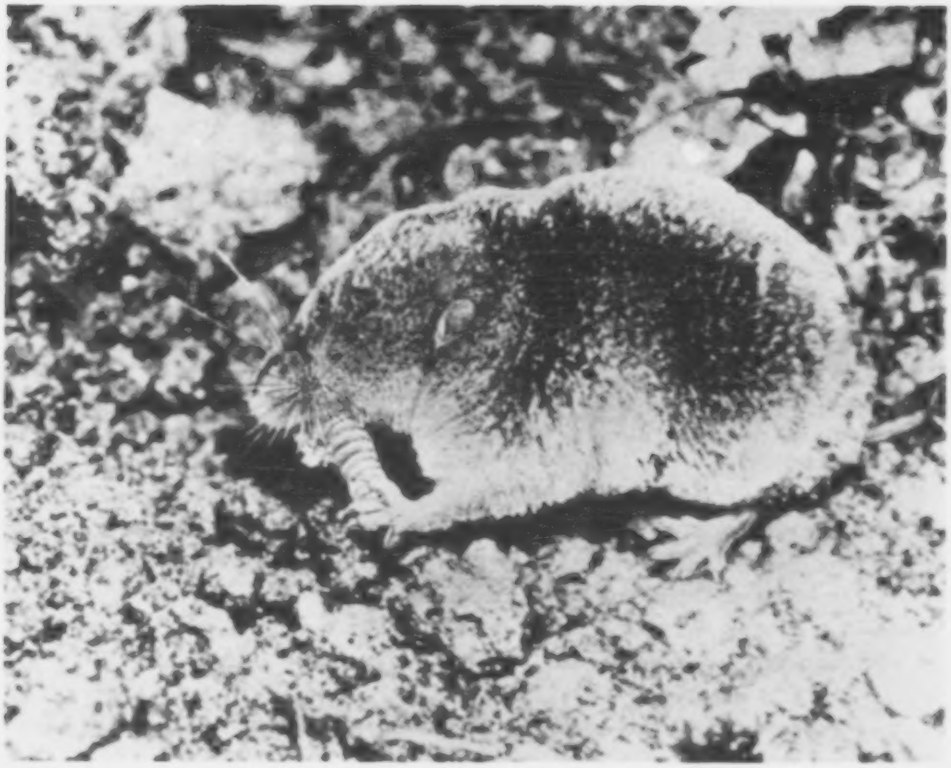
Dusky Shrew, *Sorex obscurus*

(a) Introduction

Two races of dusky shrews have been described from the Queen Charlotte Islands, both by Osgood (1901). *S. o. elassodon* Osgood is "found only on Langara, Graham, Moresby, and smaller adjacent islands in the Queen Charlotte Islands. Occurs also on some islands of the Alaskan coast north to Admiralty Island" (Cowan and Guiguet 1956). The latter include Prince of Wales, Duke, Forrester, Hecata, Kuiu, Kupreanof, Mitkof, Baranof, and Dall Islands. The same authors consider the other race of shrew, *S. o. prevostensis* Osgood, to be confined to Kunghit (formerly Prevost) Island.

In the following discussion the races found on the Queen Charlotte Islands are compared to specimens of *S. o. elassodon* from Alaska, and *S. o. longicauda* from the adjacent mainland and S. o. *insularis* from nearby mainland islands, with the intention of reconstructing the probable history of the evolution of the species within the region.

Prevostensis and *elassodon* were originally described as races of the species *S. longicauda*, but all three have since been placed as races of *S. obscurus* by Elliot (1905). In his original description, Osgood (1901, p. 35) writes that *prevostensis* is "similar to *Sorex longicauda*; tail, relative to head and body, shorter," the colour "very slightly darker than *S. longicauda*; contrast between upper and lower parts less; otherwise similar... size large, equal to *S. longicauda*; dentition slightly lighter; third unicuspid nearly equal to fourth, not about one-half smaller as in *longicauda* ... The shrews of Prevost Island differ from those of Graham and Moresby Islands to a greater degree than from the mainland species *S. longicauda*. In colour they are very dark, even averaging darker than *longicauda*; occasional specimens are deep chocolate brown both above and below. On the whole, however, they are very similar to *longicauda*, but the combination of slight characters they show can hardly be explained, except by assuming that they were produced by insular isolation. The case is much like that of *Peromyscus prevostensis*, though not so striking. In both cases the Prevost Island form is distinct from its nearest geographical ally and very closely similar to forms found at a greater distance. The very close relationship of *prevostensis* to *longicauda* seems best indicated by a trinomial name."



A dusky shrew (Sorex obscurus prevostensis) eating an earthworm.

S. o. prevostensis is "larger and darker than S. o. elassodon, with larger hind foot; skull with longer palate and broader rostrum than in that of elassodon." (Jackson 1928). S. o. insularis differs from the adjacent mainland race (longicauda) in smaller body, tail and hind foot. The skull is smaller in condylobasal length and tooth row (Cowan 1941).

(b) Material

Shrews were taken at most trapping sites, but usually a concentrated effort had to be made to secure more than a half dozen specimens. Greater success was often achieved after most of the population of Peromyscus had been removed.

The following islands of the Queen Charlotte Islands are known to have populations of Sorex obscurus, the number of animals examined in parenthesis: Langara (29), Graham (27), Hippa (12), Ogilvie (3), Queen's (1), MacKenzie (3), Chaatl (3), Saunders (4), Helgesen (7), Hibben (4), Moresby (30), Legace (1), Lina (1), Maude (1), Talunkwan (3), Tanu (1), Kunga (3), Lyell (1), Bischoff (3), Bolkus (2), Gowing (1), and Kunghit (44). A total of 184 specimens was examined from the Queen Charlotte Islands, including 15 borrowed from the National Museum of Canada and 41 from the United States National Museum.

There were several collections made on each of Graham and Moresby Islands and their localities, with numbers of specimens, are as follows: Graham Island: Masset area (5), Bradley's Ranch (4), Merle's Point (3), Peril Bay (2), Pt. Clements (2), McClinton Creek (1), Queen Charlotte City (1), and Masset Inlet (8). These were considered as one population. From Moresby Island the following localities were collected: Cumshewa (type locality of elassodon) (20), Armatieres Channel (1), Sandspit (1), Peel Inlet (1), Pacific Inlet (3), Tasu Sound (3) and Harriet Harbour (1). The first three were considered as one population, that of north Moresby Island, while the last three are treated separately as those belonging to south Moresby Island.

Specimens of shrews were examined from the coastal area to the east of the Queen Charlotte Islands from the following localities: Koeye and Neekas Rivers (19), and Townsend (21) and Smythe (24) Islands. The first two localities are situated on the mainland and are within the range of the race of longicauda. The islands support the race insularis.

Seventy specimens of elassodon and 42 specimens of longicauda were examined from southeastern Alaska. These were borrowed from the Museum of Vertebrate Zoology, University of California.

Of the Alaska material, detailed examination was performed only upon specimens from the three islands which are situated close to the Queen Charlotte Islands and which are purportedly within the range of elassodon; Prince of Wales (8 specimens), Kupreanof (9) and Forrester Island (10).

(c) Variation

In spite of the rapid growth and early attainment of maturity in shrews, Jackson (1928) considers that there is a great difference in the skulls at different ages, and that it is essential in making comparisons to have specimens of approximately the same age. He places all skulls into four classes: immature, young adult, adult, and old adult. In the present paper, the four are referred to as Age Class 1, 2, 3, and 4, respectively. For definition of the classes see Jackson (*op. cit.*)

In the present study, Age Class 2 is by far the commonest, always comprising more than 50% and usually more than 80% of the sample.

In order to examine the change in measurements with age, four of the measurements found to be most useful by taxonomists were plotted against age (Foster 1963). It was found that while the skull measurements undoubtedly change with age, the correlation is so poor that age appears to be an insignificant factor when comparing these measurements. In view of this observation, and the fact that most specimens belong to one Age Class, it will be assumed that age is not important when comparing the skull measurements of different populations of *Sorex*.

Pelage changes seasonally, with a moult in the spring and the fall, the summer pelage being generally shorter and paler than the long, dark winter pelage. The pelage also changes appreciably with amount of wear. In addition, individual variation limits the use of this character.

So far as is known, there is no sexual variation of colour, size, or proportions in any of the American soricids (Jackson, *op. cit.*)

The most important variation from the standpoint of this paper is that which exists between populations of shrews. This geographic variation is slight when compared with some mammal groups (cricetids, ursids) and could perhaps be the result of dealing with a drab-coloured group of mammals with minute, simple, skulls. *S. o. obscurus* is found with scarcely any variation from north-central Alaska to northern New Mexico. Jackson (*op. cit.*) considers that the most important factor in limiting the variation within the group is their great phylogenetic age. He writes (p. 19), "shrews are geologically among the oldest of the true placental mammals, and as such their characters are deep seated and well fixed." In spite of this, there are six races of *Sorex obscurus* confined to the islands of British Columbia and in view of the recent geological age of these islands, the importance of insular isolation in the evolution of these races is clear.

(d) Taxonomic Characters

Eight measurements were taken from each complete specimen. Three were taken in the field by the collector: the total length of the animal, the tail length, and the length of the hind foot. These measurements can not be re-checked and may sometimes be in error as a result of being measured by different collectors. The five skull measurements were taken by myself and include the condylobasal length, the length of the palate, the maximum width of the skull, the maxillary width and the length of the tooth row.

The colour of the pelage is often used to help distinguish some races of shrews, although it is of limited use as has been pointed out earlier.

(e) Analysis of the populations

Since some islands are represented by so few individuals and could not logically be included with other islands, they are excluded from statistical examination. The only islands considered are those from which there are at least 10 specimens, except when more than one island is grouped as a single sample of at least 10 specimens.

A total of 12 populations of *Sorex obscurus* is compared, seven from within the Queen Charlotte Islands and five from elsewhere. The type localities for the two Charlotte races are represented by the samples from Kunghit Island (*prevostensis*) and northern Moresby Island (*elassodon*). The other localities on the Queen Charlotte Islands from which there is a useful series of specimens include the following islands: Langara, Graham, Hippa, Ramsay, and a group of six islands scattered along the south-east side of the Archipelago, Talunkwan, Tanu, Kunga, Lyell, Bischoff and Bolkus.

On the mainland the Koeye and Neekas River samples fall with the range of *longicauda* and are grouped together for statistical treatment. Those from Townsend and Smythe Islands (*insularis*) are considered separately since each is a large sample and it should be possible to distinguish any variation between them. Since the Alaska specimens from Prince of Wales and Kupreanof Islands appear to be very similar in gross examination and have been described as belonging to the same race (*elassodon*), they are grouped together. The Forrester Island specimens, though ascribed to *elassodon* (Jackson 1928), appear to have distinctive features and are treated separately.

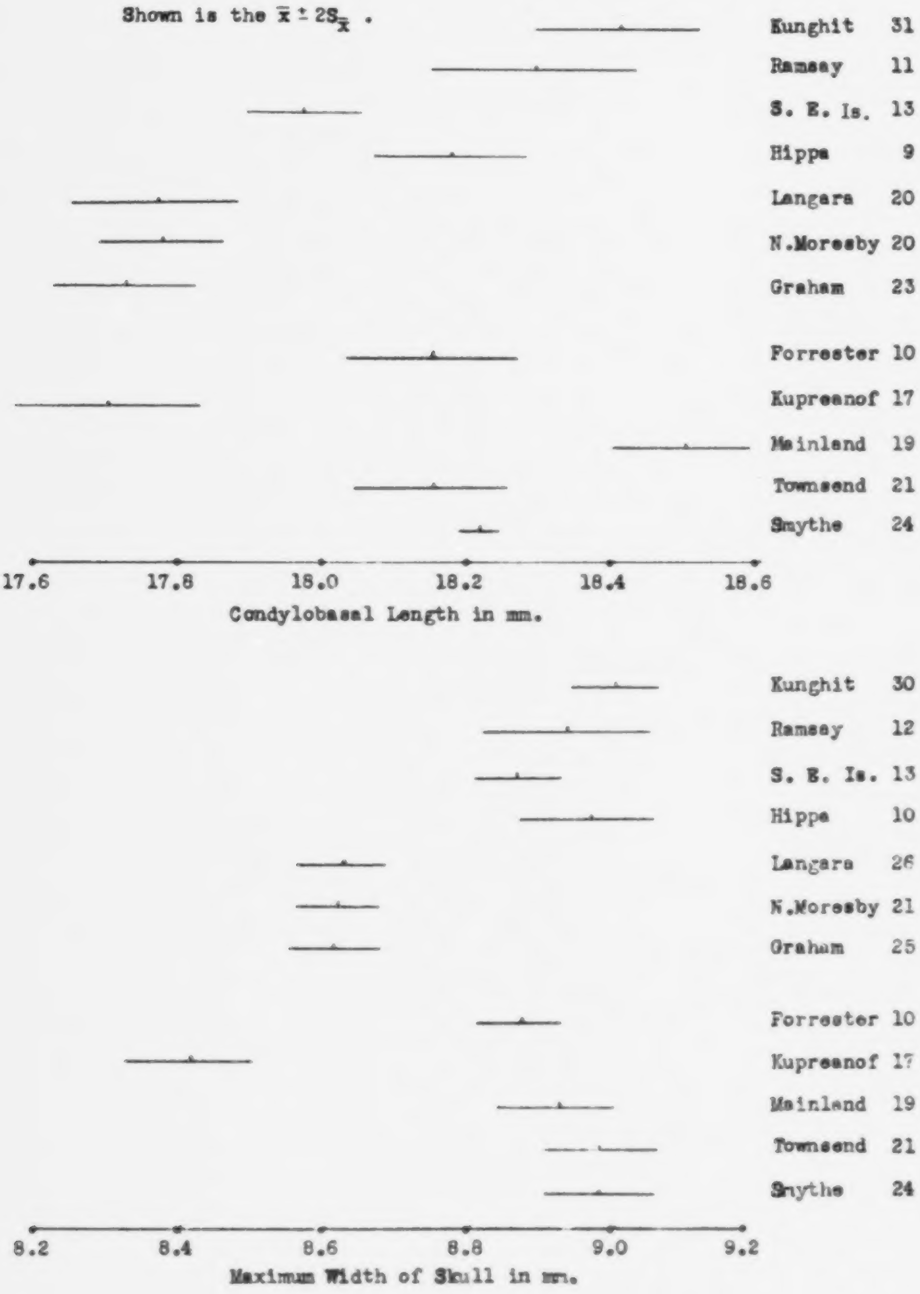
Some of the samples are not large and it is realized that most of the conclusions are tentative pending the collections of a larger series of specimens.

The statistical method employed in comparing populations is a modification of that first proposed by Dice and Leraas (1936) and developed by Hubbs and Hubbs (1953). It involves calculating the sample mean ($\bar{x}$), the standard deviation (S. D.) and the standard error of the mean (S$\bar{x}$) and plotting these on graph paper so that the samples may be readily compared. Different authors have suggested the different probabilities which should be used. Recently the $\bar{x} \pm 2\,S_{\bar{x}}$ has been most commonly used (Hagmeier 1955, Sheppe 1958) and is employed herein (Figure 4). Hibbs and Hubbs (*op. cit.*) present a means of interpreting the figures in terms of statistical significance. Roughly, if the $\bar{x} \pm 2\,S_{\bar{x}}$ of two samples do not overlap, the difference between the samples is statistically significant at the 95% level. If the $\bar{x} \pm 3\,S_{\bar{x}}$ do not overlap the significance is at the 99% level or better.

Figure 4 shows the $\bar{x} \pm 2\,S_{\bar{x}}$ for each sample for four skull measurements, the condylobasal length, the maximum width of the skull, the maxillary width, and the length of the maxillary tooth row. Beside each locality is the number in the sample. These numbers are not necessarily the same for each measurement since not all four measurements could be taken on defective skulls. "S. E. Is." signifies the six islands which make up the sample from the south-east Islands of the Queen Charlotte Islands, while "Kupreanof" includes specimens from both Kupreanof and Prince of Wales Islands. "Mainland" is represented by the Koeye and Neekas River samples.

In Figure 4, consider the first seven samples, that is, those from the Queen Charlotte Islands. The type locality of *elassodon* is represented by the northern third of Moresby Island

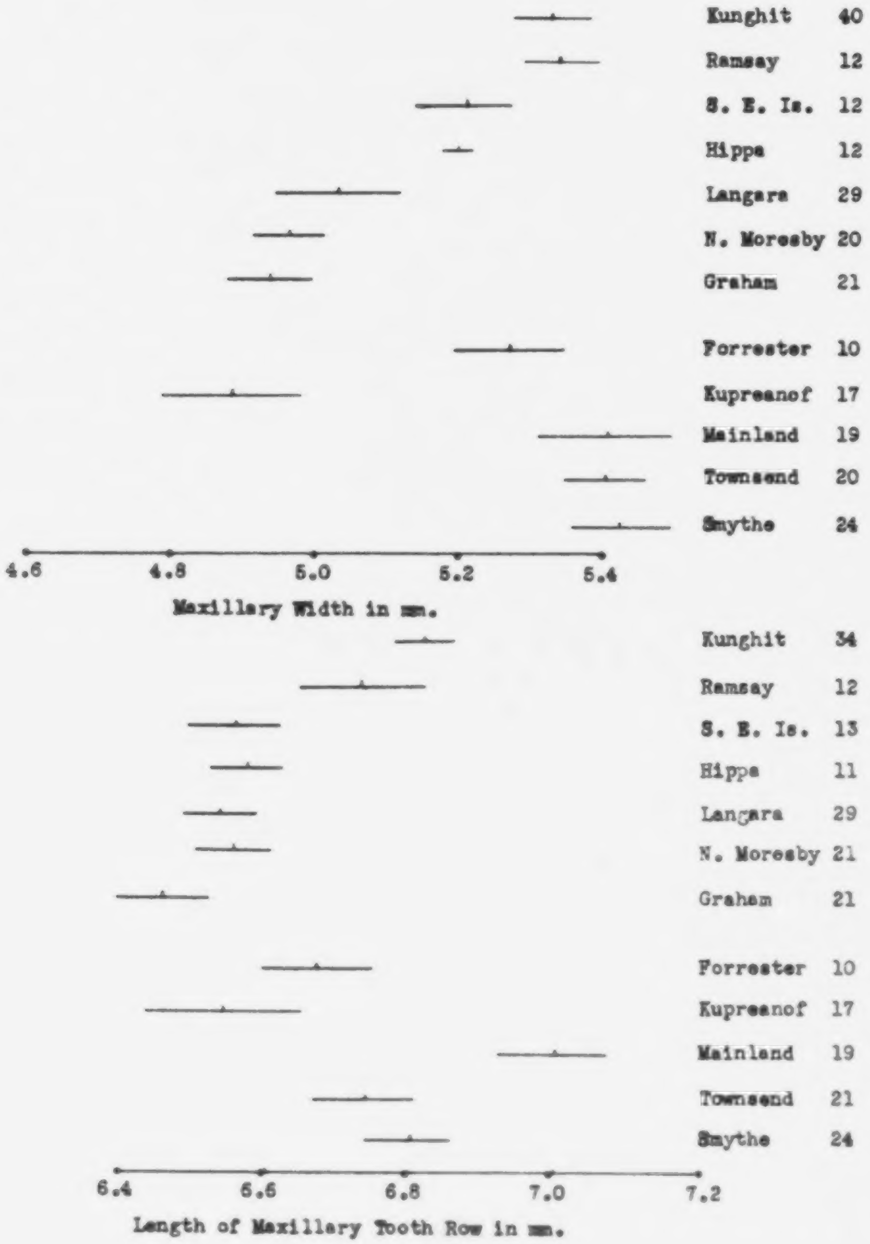
Figure 4: Comparison of some skull measurements of *Sorex obscurus*.



Shown is the $\bar{x} \pm 2S_{\bar{x}}$.

Figure 4 continued: Comparison of some skull measurements of *Sorex obscurus*.

Shown is the $\bar{x} \pm 2S_{\bar{x}}$.



and of *prevostensis* by Kunghit Island. These two samples are widely separated (even at the $\bar{x} \pm 3 S_{\bar{x}}$), in all four skull measurements, *prevostensis* being consistently larger than *elassodon*. *Prevostensis* is also generally browner on the belly than *elassodon* individiuals ranging from chocolate to the pale gray-brown of *elassodon*. These distinctions are in accord with those given by Osgood (*op. cit.*).

It is now necessary to decide into which race the other five samples fall, or whether new races are necessary to account for the observations.

The samples from Graham and Langara Islands clearly belong with the north Moresby Island race (*elassodon*), since the $\bar{x} \pm 2 S_{\bar{x}}$ of all four measurements widely overlap those of this race. The pelage is also very similar. Placing these three samples within the range of *elassodon* is in accordance with earlier literature.

The sample from Ramsay Island appears to belong to *prevostensis* when each of the four skull characters are considered. However, the pelage lacks the dark belly pigment of *prevostensis* and is identical with that of *elassodon*. While one might consider this difference sufficient to warrant the description of a new race, I believe that almost every island population could be so characterized given sufficient number of specimens, but to do this would be purposeless, since it is relationships which are being sought, not the proliferation of races. Accordingly, the Ramsay Island specimens are grouped as *prevostensis*, realizing that while they are most similar to that race, they are not typical forms.

The six islands which make up the sample from the south-east islands are intermediate between the two races in condylobasal length and maxillary width, with the maxillary length of the tooth row not significantly different from *elassodon* and the maximum width of the skull not significantly different from *prevostensis*. Little more can be said about the populations living on the south-east Islands until a larger series of specimens is taken from each Island.

The small sample from Hippa Island indicates that this population is allied to *prevostensis* in the condylobasal length and maximum width of the skull, but to *elassodon* in the length of the maxillary tooth row and intermediate between the two races in the maxillary width. The pelage appears to be identical with that of *elassodon.*

The dusky shrews from Forrester, Kupreanof and Prince of Wales Islands of the Alexander Archipelago have been ascribed to *elassodon* by all authors (Jackson 1928, Cowan and Guiguet 1956, Hall and Kelson 1959). Figure 4 indicates that this is justified for the sample from Kupreanof and Prince of Wales Islands since three of the four measurements are not significantly different from the type sample. However, the maximum width of the skull is significantly smaller, while the pelage appears to be identical with other *elassodon.*

Specimens from Forrester Island, heretofore ascribed to *elassodon*, seem more similar to *prevostensis.* The maxillary width is not significantly different, while the other three skull characters are on the border of being significantly smaller than *prevostensis.* All measurements except the length of the maxillary tooth row are significantly larger than in any of the three *elassodon* samples; however, the pelage appears to be similar to *elassodon.*

The sample of specimens from the "mainland" (Koeye and Neekas Rivers, *longicauda*) is very similar to *prevostensis*, there being no significant difference in condylobasal length, maximum width and maxillary width. The length of the maxillary tooth row is significantly larger at the 95% but not the 99% level. On the other hand, the difference in pelage is consistent: the belly fur is browner in *prevostensis* in both summer and winter pelages, having the effect of lessening the contrast between the dorsal and ventral surfaces. These observations are in accord with Osgood (1901) who writes that *prevostensis* is slightly darker than *longicauda*, with dentition slightly lighter. The difference in size of the third and fourth unicuspid teeth, described by the same author, is not discernible in the present samples.

The specimens from Ramsay Island are almost perfect intergrades between *prevostensis* and *longicauda* in pelage, the skulls of the three being very similar except for the difference in maxillary tooth row, a measurement in which Ramsay and Kunghit specimens are significantly distinct from *longicauda.*

The samples of *insularis* from Townsend and Smythe Islands are not significantly different from one another in all four skull measurements. They are both significantly smaller than *longicauda* in condylobasal length and length of the maxillary tooth row as has been described by Cowan (1941).

To summarize, it appears that there are two well characterized races of shrews on the Queen Charlotte Islands, *prevostensis* on Kunghit Island and *elassodon* on Graham, Langara and the northern end of Moresby Island. Specimens from Ramsay Island closely resemble *prevostensis* in size, but *elassodon* in colour. The other samples from the Queen Charlotte Islands appear to be intermediate to the two races.

Specimens from Forrester Island are most similar to *prevostensis*, while those from Kupreanof and Prince of Wales Islands are almost identical with *elassodon*. *Prevostensis* is very similar to *longicauda* apart from colour; *isolatus* is also similar but is significantly smaller in two skull measurements.

It appears that in the samples under discussion, it is *elassodon* which is most distinct, the others being more nearly similar to one another.

The differences recorded above could either have a genetic basis, or be the result of the soma of the individual responding to the particular environment. Unfortunately, direct evidence from breeding experiments is lacking and it is necessary to try to seek the answer elsewhere.

It has been shown earlier (Huxley 1932, Cowan 1941), that there is some support for the view that insularity produces stunting and change in proportions in several cervids and that this syndrome is occasioned by the effect of the environment on the individual soma, rather than it having a genetic basis.

Studying this species of shrew in the same general area, Cowan (*op. cit.*, p. 107) writes that "if the size differences observed on certain islands are the direct result of the environmental action upon the soma of each individual it is difficult to account for the presence of differentiated and undifferentiated populations living on islands of identical type separated by but a very narrow water barrier. It is equally difficult to account for the varied pelage colours displayed by the different populations on closely adjoining islands.

"Therefore it seems more logical to assume that the observed differences are due to the building up of forms with superior viability under the selective conditions imposed by insular isolation."

If some unifying pattern can be discerned among the shrews, then it might indicate the underlying directive force. Cowan (op. cit.) has studied the same species on the mainland coast of British Columbia and writes, "In general we have found that this shrew living under insular conditions tends to develop shorter body, tail and hind foot and a skull smaller in all features but interorbital breadth." However, on the Queen Charlotte Islands, the forms on small islands tend to have larger skulls than do those on the nearby "mainland" (Graham and Moresby Islands). There appears to be no relationship between extent of environment and size of shrew since large shrews are found on the mainland (longicauda), Kunghit Island (15 miles long) and Hippa Island (2 miles long). Neither size of the animal, nor its colour seems to change with latitude. Only one conclusion might be possible; all the island forms studied have a shorter maxillary tooth row than those found on the mainland.

No environmental factors can be found which have selected for the variations discernible between the samples, and this is an admission of our profound ignorance of the factors involved.

(f) Discussion

With the waning of the Vashon glaciation about 10,000 years ago, most of British Columbia and Alaska were opened for repopulation by shrews. It has already been shown that Sorex obscurus might have survived in the refugia on the Queen Charlotte Islands, in which case it, too, could have spread out from this locus to colonize new areas. The species might have even spread to the mainland, though in view of the contrary direction of the currents, and the likelihood that waifs would have had a better opportunity on the virgin Queen Charlotte Islands rather than the rapidly colonized mainland, the reverse is more likely to have occurred. It is possible that one of the two races of shrews on the Queen Charlotte Islands was derived from the population in the refugia, while the second arrived from the mainland subsequent to the retreat of the glaciers. On the other hand, if shrews were absent from the Charlotte refugium, then all forms have come from the mainland in recent times. The discussion will proceed with the analysis of these two basic alternatives, each in turn having further alternatives which could be multiplied almost ad infinitum. Only those theories with a minimum number of suppositions will be considered in accordance with Occam's Razor.

Shrews were present in the Charlotte refugia.

(1) Of the two races of shrews on the Queen Charlotte Islands, *prevostensis* is more similar to the races presently living on the mainland (*longicauda*, *insularis*); as a consequence, *elassodon* is more likely to be the progeny of the form which lived in the refugia. Its distribution presently encompasses the probable refugia areas, while *prevostensis* is confined to Kunghit and perhaps Ramsay, Hippa, Forrester and other islands.

If this is so, then one would conclude that after the retreat of the glaciers, the *elassodon* type extended its range over most of the Queen Charlotte Islands, spreading to the Alexander Archipelago by chance or on a land bridge. The ancestors of *longicauda*, on the other hand, spread northwards from the refugium in Washington, reaching many of the coastal islands, and becoming slightly distinct on some. The transportation of waifs by Indian canoes or rafts carried *longicauda* to Kunghit and a few other islands where they became sufficiently distinct from their ancestor to be described as a separate race.

Indian canoes likely played the most important part in transporting shrews from one island to another, since the activity of the Haida Indians extended throughout the area, as explained earlier. The *prevostensis*-*longicauda* type transported by chance to Graham and Moresby Islands would have encountered a large population of *elassodon*, and their characteristics would have become rapidly diluted. Those *prevostensis* carried to the smaller islands would have encountered a much smaller, or perhaps, no population of *elassodon*. It is suggested, therefore, that the islands from which the samples of shrews are most like *prevostensis*, are those islands which had no population of *elassodon*, and on which the new arrivals consequently retained most of the characteristics of their ancestors. Those islands with forms resembling *prevostensis* to a lesser degree were already populated with *elassodon* and a hybrid resulted.

Hence, under this theory, it seems likely that the variation between *longicauda*, *prevostensis* and *elassodon* found on the islands was initiated by sporadic transport by Indian canoes but with genetic drift and selection under differing environmental pressures also perhaps playing a part.

(2) As an alternative explanation it is possible that the ancestor to *prevostensis*, rather than *elassodon*, lived in the refugia and at the close of glaciation, spread over most or all of the Queen Charlotte Islands. Later, *elassodon* was able to reach the Islands from a hypothetical refugium in the Alexander Archipelago or on the mainland, and subsequently spread throughout most of the islands displacing *prevostensis* and leaving it as a relict population on Kunghit, Ramsay, Hippa and Forrester Islands.

There are several serious difficulties in this explanation. In the first place there is no good evidence that there was an unglaciated area in southeast Alaska or on the nearby mainland which would have been suitable as a refugium to enable this species to survive during the last glaciation. Further, there seems to be no explanation as to why *elassodon* should have displaced *prevostensis* on Graham and northern Moresby Island. In addition, the close morphological relationship between *prevostensis* and *longicauda* would be difficult to explain under any hypothesis requiring their separation for some 100,000 years. Finally, the samples of *prevostensis* from Kunghit, Ramsay, Hippa and Forrester Islands, while being similar to one another, are each recognizably different in at least one characteristic and, therefore, do not obviously belong to one ancestral population.

(3) A third possible explanation is that both *elassodon* and *prevostensis* have evolved from a common ancestor which lived on the Islands during glaciation. *Prevostensis* evolved in isolation, perhaps on Kunghit Island, appearing on other islands either as a result of dispersal in Indian canoes, or by parallel evolution.

While this explanation has some merit, it is remarkable that *prevostensis* should so closely resemble *longicauda* of the mainland, without there being some direct and recent phylogenetic connection. In addition, the fact that *elassodon* is more different from *prevostensis* than *prevostensis* is from other shrews in the area, makes it unlikely that the two should have recently evolved from a common ancestor.

Shrews were not present in the Charlotte refugia.

(4) The most likely shrew to have reached the Queen Charlotte Islands after glaciation is one resembling the present mainland race *longicauda*, since as explained earlier, there is no known refugium near the Islands which would have been suitable for *elassodon*. Hence in this explanation it is assumed that a

longicauda-type reached the Queen Charlotte Islands evolving into the races prevostensis and elassodon. The main difficulty with this explanation lies in accounting for the fact that the differences between elassodon and prevostensis are greater than those between the latter and other shrews in the area, and it is thus unlikely that the two have recently evolved from a common ancestor.

Of all the explanations, (1) is in closest accordance with the meagre facts presented. Future work should examine more distant races to see whether a form similar to elassodon can be discovered. If such is found, this theory would be weakened. Larger collections from many islands could help clarify dubious assumptions in the present work and most important would be a study of the environmental factors which are important in the evolution of shrews.

(g) Summary and Conclusions

Soricids are considered to be primitive mammals, not readily subject to change. However, in the region under study is a multiplicity of insular forms indicating the importance of isolation of small populations as a factor in their evolution. Circumstantial evidence indicates that the forms are genetically different, though the basis for the selection of the different characters is unknown. The only discernible trend in the samples under study concerns the length of the maxillary tooth row which is significantly shorter in all insular populations.

While most of the smaller islands on the Queen Charlotte Islands each has a slightly different form of shrew, it is felt that these all belong to either of the major genotypes of elassodon or prevostensis and that the description of new races is unwarranted. The conclusion to limit the number of races to two is strengthened by the most plausible theory for their evolution in the area. It is thought that elassodon is a population which has been on the Queen Charlotte Islands since pre-Vashon times and that prevostensis is a recent arrival and a descendant of longicauda. Hence, the two stocks should be represented as at present until some forms, which may be in a nascent state, become more distinct.

The collection of larger samples from many islands and the description and analysis of the ecologic and genetic factors which play a part in the proliferation of the forms of this species, are important tasks which could fill in many of the gaps in the present study.

Deer Mice, *Peromyscus* spp.

(a) Introduction

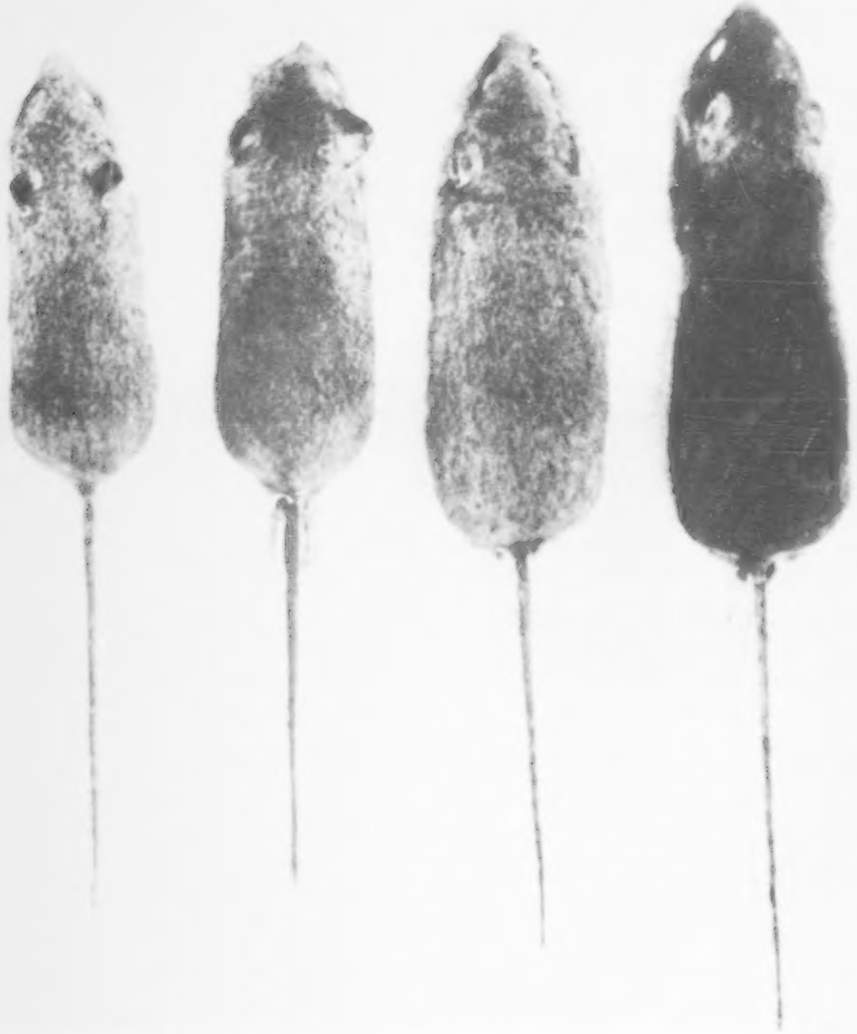
Deer mice are the only rodents native to the Queen Charlotte Islands. They have been described as belonging to two species *Peromyscus maniculatus*, widely spread across most of North America and, on the Queen Charlotte Islands, found on the main islands, Graham and Moresby; and *P. sitkensis* a species with a most disjunct distribution scattered islands in the Alexander Archipelago of Alaska and most outer islands of the Queen Charlotte Islands.

P. maniculatus keeni (Rhoads) was originally described as a distinct species (*Sitomys keeni*) by Rhoads in 1894 from an alcoholic specimen taken at Masset, Graham Island. Bangs (1897) placed *keeni* in the genus *Peromyscus* and Osgood (1909) further changed it to a subspecies of *P. maniculatus*, the position it now holds. Osgood (1909, p. 55) writes "This mouse is of the same general type as *P. m. oreas* of the Puget Sound region and *P. m. hylaeus* of the islands and coast of southeastern Alaska. It is most closely related to *hylaeus*, being distinguished only by slight original characters. Since these characters, although reasonably constant, vary slightly towards *hylaeus*, it seems fitting to include *keeni* among the numerous subspecies of *maniculatus*." Osgood found *keeni* to extend over the length of Graham and Moresby Island.

P. sitkensis prevostensis was originally described as *P. prevostensis* by Osgood (1901) from a large series of specimens taken on Prevost (now Kunghit) Island, Queen Charlotte Islands. The same author later (1909) considered *prevostensis* to belong to the species *sitkensis*, resident on a few islands in Alaska (Baranof, Chichagof, Forrester, Dall and Duke), hence the present name *P. s. prevostensis*. Until the present study, this race was considered to be confined to Kunghit, Frederick and Hippa Islands of the Queen Charlotte Islands.

The two species of mice on the Queen Charlotte Islands are described as being readily separable on the basis of size, *prevostensis* averaging almost twice the weight of *keeni*.

The present work has shown that a form similar to *prevostensis* exists on the outer islands which contain this genus, while *keeni* is confined to the two main islands plus a few centrally located islets. Some populations of mice (e.g.



Specimen skins of deer mice (from left to right):

Peromyscus maniculatus keeni
P. m. rubriventer
P. m. sitkensis
P. m. sitkensis, melanistic form
From Frederick Island

Hippa Island *prevostensis*) resemble far more closely distant populations (e.g. Kunghit I. *prevostensis*, 150 miles to the southeast) than they do a closer population, (e.g. Peril Bay, Graham I. *keeni*) only one-half a mile away (see Figure 1). To explain such a distribution will require critical analysis. Similarly, the wider problem of the highly disjunct distribution of the species *P. sitkensis* as a whole must be explained: its distribution spanning hundreds of miles from Chichagof Island to Kunghit and broken by members of another closely related species, *P. m. hylaeus* and *P. m. keeni*.

Cowan (1935) has advanced the theory that *P. sitkensis* is a relict population from the previous interglacial age which was able to find refuge in unglaciated areas during the Vashon ice advance. Such a refuge apparently existed on the Queen Charlotte Islands themselves. It is theorized that following glaciation the species was able to extend its range considerably beyond the present and later when *P. maniculatus* immigrated into the area from the refugium in the United States wherever *maniculatus* met *sitkensis* the latter was forced into extinction as a result of the superior competitive capacities of the continental form. The fact that the two species never occur sympatrically lends weight to this interpretation.

This same "relict" theory has been advanced to explain the distribution of some of the small mammals in Britain and Europe by Barrett-Hamilton and Hinton (1914), Hinton (1926), Matthews (1952) and Zimmerman (1950). However, a second school has recently cast doubt upon this interpretation (Steven 1953; Delany and Bishop 1960; Cook 1961; Corbet 1963). They contend that the so-called relicts are really recent developments, reflecting some selecting feature in the environment. Further evidence against the relict nature of periferal populations is supplied by Lamotte (1951) and Cook and Peake (1960) working with *Cepaea nemoralis*, and Ford (1955) working with *Maniola jurtina*.

It will be necessary to attempt to assess which of the two theories is more likely to apply in the present situation, or whether the facts necessitate a new explanation.

(b) Material

Specimens of *Peromyscus* were collected at every opportunity and at every location possible. In general effort was made to obtain at least a dozen adult individuals from each trapping site and more than a dozen individuals were skinned for the Museum collection, if the opportunity permitted. Sometimes only the skull could be saved, and occasionally only the measurements.

The following islands of the Queen Charlotte Islands are known to have populations of *Peromyscus* (number of animals examined in parenthesis): West Coast (north to south), Frederick (28), Hippa (27), Marble (31), Helgesen (9), Saunders (7), Hibben (12), Anthony (23), Gordon (23), and Kunghit (55). East Coast Islands; Louise (34), Reef (13), Talunkwan (5), Tanu (3), Lyell (3), Bischoff (11), Hotspring (17), Ramsay (22), Poole Inlet (4), East Copper (6), George (13), Bolkus (14), and Rankine (12). The main islands, Graham (283) and Morseby (155) have a few islands enclosed within them: Wathus (6), Harrison (26), Lina (38), Maude (4), and Chaatl (17). A total of 910 *Peromyscus* were examined from the Queen Charlotte Islands.

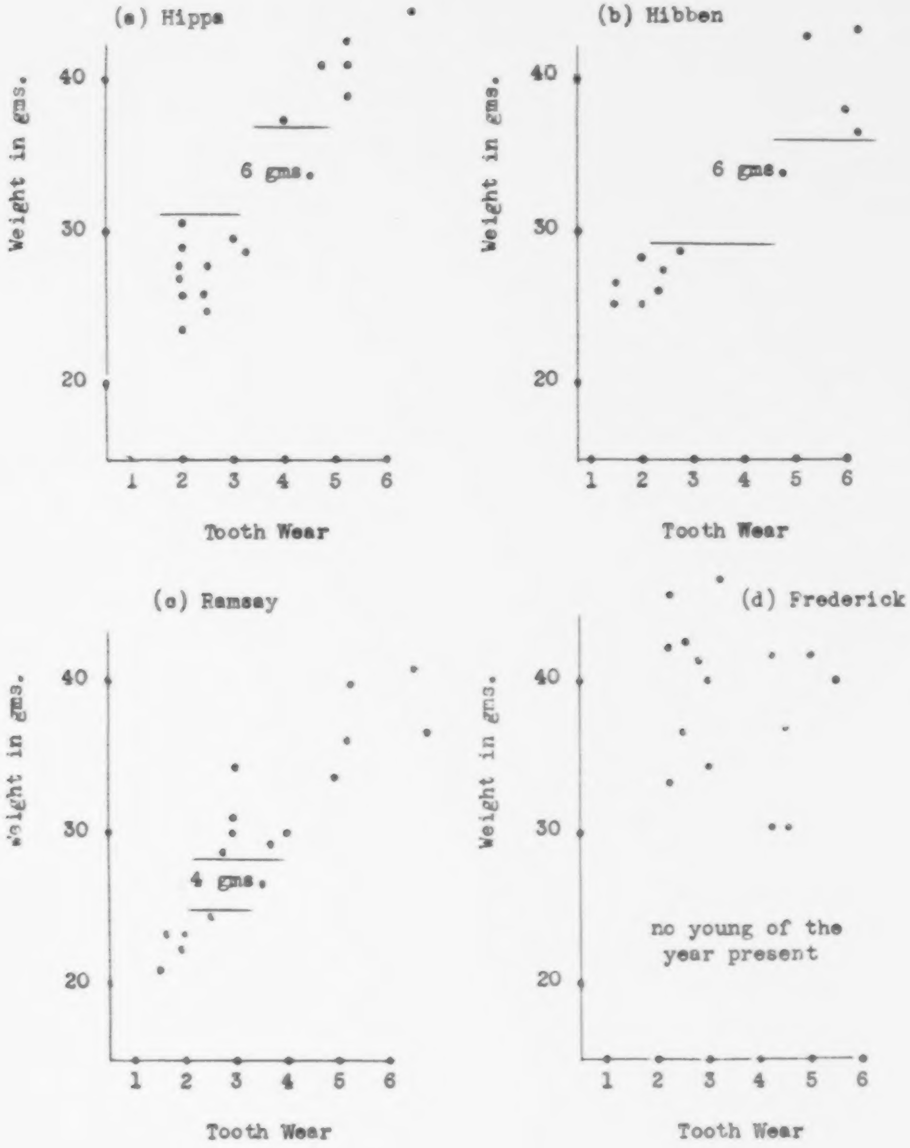
For purposes of comparison, specimens of *Peromyscus* from the following localities outside the Queen Charlotte Islands were included: Alexander Archipelago including Baranof (16), Chichagof (11), Admiralty (25), Mitkof (24), and Forrester (10). British Columbia: Banks (13), Calvert (25), Hunter (24), and Goose (22). A total of 1080 *Peromyscus* were examined in this survey.

The location of the islands in the Alexander Archipelago is shown in Figure 2 and these islands represent the following forms: *P. m. sitkensis* on Baranof and Chichagof, *P. s. oceanicus* on Forrester, and *P. m. hylaeus* on Admiralty and Mitkof.

Banks, Calvert, Hunter and Goose Islands lie next to the mainland east and south-east of the Queen Charlotte Islands. The following forms are found on these islands: *P. m. macrorhinus* on Banks and Calvert, *P. m. rubriventer* on Hunter and *P. m. pluvialis* on Goose.

The following institutions lent specimens of *Peromyscus* from the Queen Charlotte Islands: National Museum of Canada, 23; American Museum of Natural History, 7; British Columbia Provincial Museum, 72; U.S. National Museum, 47; and from Alaska: the University of California, Museum of Vertebrate Zoology, 47 *P. m. macrorhinus*, 117 *P. m. hylaeus*,

Figure 5: Tooth wear (age) plotted against weight (size) for four small island samples of Peromyscus collected in the summer.
Pregnant females excluded.



15 *P. s. oceanicus* and 46 *P. s. sitkensis.*

(c) Variation

Age is a most important kind of variation in any species and its consideration is basic in univariate analysis for systematic purposes or to an understanding of the life history of the animal. Satisfactory age criteria must be established so that comparisons may be restricted to individuals in a similar state of development. Also, the age structure of different populations may be compared. The criteria applied in this study is that of degree of tooth wear.

Although naturally tooth wear takes place gradually and not in steps, for the purposes of comparison, it was found convenient to designate six age classes into which all animals fall. The classes, from youngest to oldest, are as follows: 1: M3 (third upper molar) not fully erupted; 2: M3 fully erupted but showing little or no wear; 3: M3 flattened, M1 and M2 showing little sign of wear; 4: M2 flattened; 5: M1 flattened; 6: all molar teeth very badly worn.

Group 1 represents the early juvenile stage wherein the animal is still in its juvenile pelage. In Group 2 most of the animals have gained their adult pelage and have mostly been born in the summer in which they were caught. This is deduced from the fact that when a size measurement (weight) is plotted against tooth wear, generally two clusters of points result (Figure 5, a, b): the lower are smaller animals with the tooth wear in Groups 1-3, and the upper group composed of larger animals with tooth wear Groups 4-6. Pregnant females have been excluded. The best size measurement is the weight of the animal and often can be taken as an indicator of age. Unfortunately many collectors do not weight their specimens, and in order to compare their specimens another size measurement must be used. Figure 6 shows body length plotted against tooth wear for the same population as in Figure 5. The discrimination between the two groups is not nearly so distinct and relies on tooth wear diagnosis, which is a rather subjective measurement and consequently open to error. Animals in Groups 4-6 were born in a summer previous to that when caught. Specimens from Group 6 are almost certainly in their third summer or older. Individual *Peromyscus* have been kept in captivity until they have died of "old age" when over 7 years old (Dice 1936). While generally the specimens separated into two clusters between Groups 3 and 4 (Figure 5, a, b), sometimes animals which were apparently

Figure 6: Tooth wear plotted against body length for the same four samples as shown in Figure 5. Numbers within the graphs indicate the weight of the specimen when known.

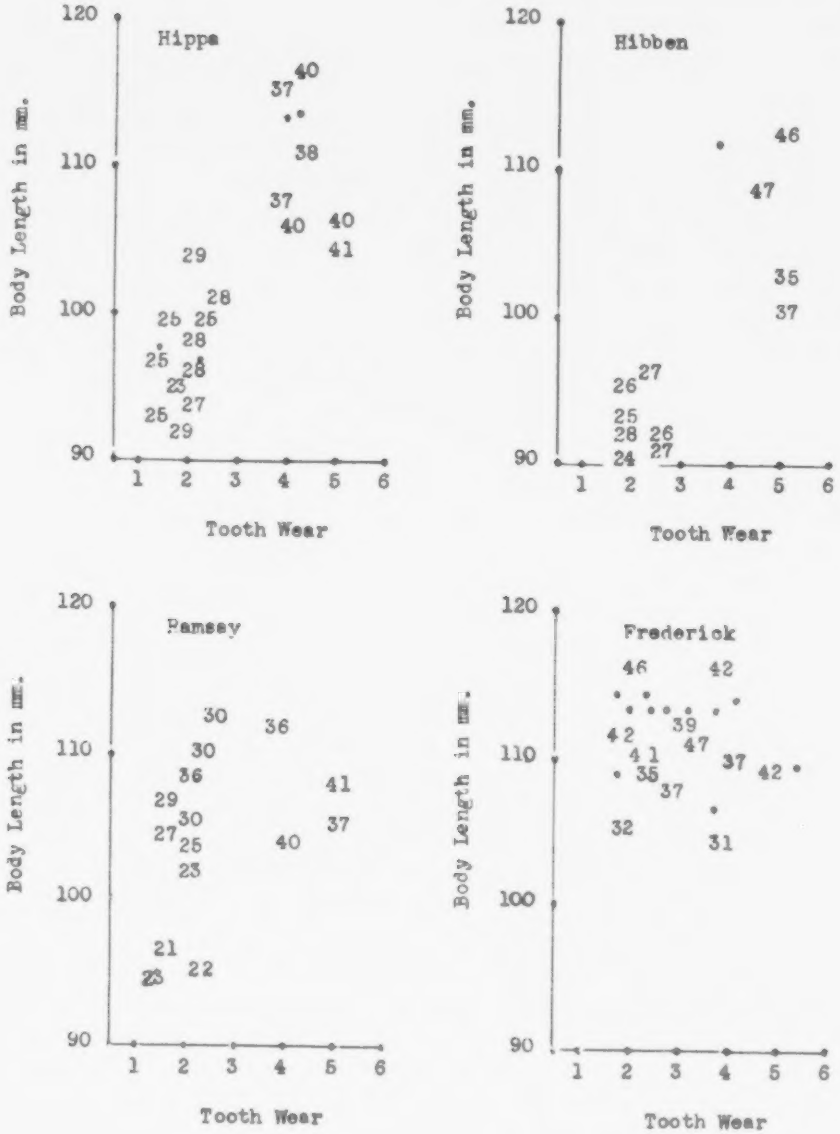
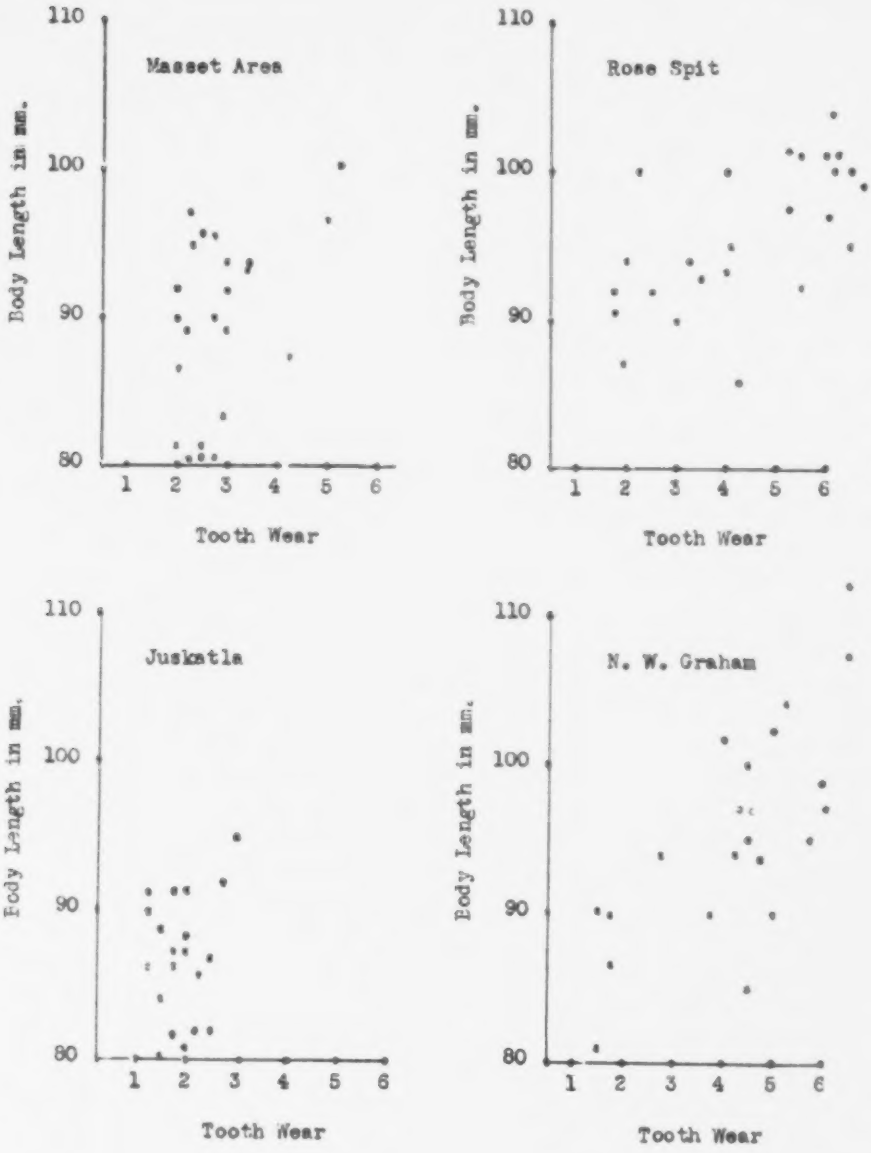


Figure 7: Tooth wear plotted against body length for samples from Graham Island. All specimens were trapped during the summer.



in their second summer fell in tooth wear Group 3 (Figure 5, c) or even in Group 2 (Figure 5, d). At other times no natural division could be discerned between the young and old groups (Figure 7). This is especially true for many samples from Graham and Moresby Islands. The absence of separation could be explained if the breeding season were much longer on the two large islands thus making a greater overlap between the age classes; however, I have no evidence that this is so and during my two summers on the islands there was little evidence of breeding observed.

A second possibility which could explain this phenomenon is that on the large islands (Graham and Moresby) there might be more genetic variation eliciting greater size variation in a given age class of the mice. The suggestion that larger populations show more genetic variation within them than do small, has been made by Carson (1955) and Ford (1955).

Samples in which the division between young of the year and those older is in doubt have been arbitrarily divided between tooth wear Groups 3 and 4. By so doing, the first group will be mostly composed of young born that summer (subadults), while the second group should contain only those in their second summer or older (adults). While an equal distance is placed between the age groupings in the Figures, there is no scientific basis for this. Until there is a series of specimens of known age raised in the wild, this arbitrary method will have to suffice. Even animals raised in the laboratory may prove to be misleading as both tooth wear and skeletal development have been shown to develop atypically under laboratory conditions (Foster and Peterson 1961).

Deol and Truslove (1957) carried out extensive studies on the variation found in an inbred line of mice (C57BL) as a result of providing them with four different diets, and a control. The four diets (oats, barley, wheat, and buckwheat) all had deleterious effects on the skeletons of the mice in the majority of cases, oats affecting the skeleton the strongest. Barley is by far the poorest diet for general health, although it has a comparatively small effect on the skeleton. Quite clearly, then, diet can significantly alter the mouse in general and skeletal parts in particular. While the mice undoubtedly eat different food on the beach from that obtained in the forest, the result of so doing is not investigated in the present study.

Different diets may wear down teeth at different rates. Beach inhabitating mice would tend to have a more silicious diet than their counterparts living well back within the forest. If such a diet wears down the teeth faster than does the forest diet, this could explain why many mice were caught on the small islands with badly worn teeth since they were generally trapped near the beach. Beach areas on Graham and Moresby Islands also frequently yielded mice with worn teeth. Those animals living in the grasses at the tip of Rose Spit on Graham Island are particularly noteworthy for having their teeth badly worn. If these are young animals, as approximately deduced from their pelage and size, then it might be concluded that the diet was having an effect; on the other hand, if they have adult coats and are of adult size, it may be surmized that diet is not having a significant effect.

From the data taken at Rose Spit it appears that all specimens showing worn teeth also have adult pelage, and as may be seen in Figure 7, most animals with worn teeth are also large. The samples from Masset and Juskatla were taken in a forest area and those from Rose Spit and Northwest Graham Island from the beach. Hence it is concluded that the presence of worn teeth in the populations is primarily indicative that the animals are older.

Table 1 lists the distribution of Peromyscus with badly worn teeth on the Queen Charlotte Islands as follows: the location, the number of specimens from the location, and the percentage of old mice, Groups 5, 6, in the sample. While these statistics would be affected by the time of the year the animals are taken, all were taken in the four summer months so any bias is assumed to be small. The figures could be influenced by an age fluctuation which occurs over the years within the populations and which differs in different locations at a given time. However, if some pattern can be discovered among the figures, perhaps it indicates the real cause.

It was stated earlier that mice with worn teeth were usually trapped on or near the beach. One must often trap in such localities on the smaller islands, but on Graham Island it is possible to trap in the interior. If all mice collected within a few hundred yards of the beach are aged (N = 540), 16% belongs to Groups 5, 6. For the mice collected in the interior of the forest (N = 61), 0% are in Groups 5, 6. These statistics give a clear indication that mice may live longer on beach areas.

Table 1:

Distribution of *Peromyscus* with badly worn teeth on the Queen Charlotte Islands.

Location	Number	% tooth wear Groups 5, 6	Location	Number	% tooth wear Groups 5, 6
WEST COAST ISLANDS			CENTRAL ISLANDS		
Frederick	28	11	Wathus	6	0
Hippa	22	9	Harrison	14	0
Marble	22	50	Lina and Maude	8	0
Chaatl	16	35			
Saunders	7	14			
Helgesen	8	50			
Hibben	12	25	GRAHAM AND MORESBY ISLANDS		
Anthony	23	9			
Gordon	12	75			
Kunghit	53	13	Rose Spit	26	50
			Masset Area	28	3
			N. W. Coast of Graham	23	39
EAST COAST ISLANDS			Juskatla Area	37	0
			Tlell, Lawn Hill	15	0
			Charlotte, Skidegate	30	0
Louise	24	17	Sandspit	17	0
Reef	12	0	Cumshewa	26	4
Takunkwan	5	0	Peel Inlet	17	0
Bischoff	11	26	Tasu	19	17
Hotspring	18	0			
Ramsay	16	13	Harriet Harbour	18	0
Bolkus	14	0	Rose Harbour	8	0
George	13	0			
Copper	13	0			
Rankine	12	0			

Table 1 shows where the old mice are distributed. The west coast islands predominate, as do the few localities on the west coast of Graham and Moresby Islands and Rose Spit.

In order to gather more evidence, I computed the age of Peromyscus from the following British Columbia Islands: Duncan, Doyle, Nigei, Balaclava, Hurst, Heard, Triangle, Sartine, Lanz, Cox, Spider, Texada, Moore, Reginald, Goose, Smythe, Campbell, Townsend, Calvert, Hope, Hunter, Table, Dufferin, and Denny. They were compared with mainland populations aged by Sheppe (1958). For age Group 5, 6 island specimens (N = 34) comprise 9.0%, mainland (N = 774), 3.5%. Thus the same trend is apparent on other islands. Its possible significance will be discussed in a later section.

Figure 5 shows that older animals are usually larger. It was found (Foster 1963) that many of the measurements increase isometrically in those mice that are old enough to be caught in traps. However, palatine slit length grows little within trapable age and this also holds true for the hind foot, interorbital width, and length of the molar row. The other measurements show considerable variation with age in the mice caught.

In future discussion body length will be the most important single measurement since it is always obtainable and indicates size almost as well as does the weight. Sometimes the mean body length of one sample will be compared with that of another. Since the body length continues to increase with age, the age composition of the samples could affect the comparison. It is found that full adults (Groups 4, 5,6) have longer body lengths than subadults (Groups 2, 3) by the following percentages: Frederick I., 1.4%, Kunghit I., 3.2%, Ramsay I., 9.6%, Reef I., 5.8%, Masset, 6.8%, Tasu, 3.3%, Skidegate, 5.6%, Rose Spit, 6.0%, and Trial I., (near Victoria), 5.0%. Thus if two samples are compared for their body lengths, up to 10% of the difference could be accounted for by age.

Sexual variation in the genus is apparently unimportant (Osgood 1909, Sheppe 1958).

The most meaningful differences between populations are those with a genetic basis so that these will be most useful to ascertain. Some populations of Peromyscus (e.g. Bischoff I.) show differences within populations which are apparently genetic in nature. This natural variation within the wild population is also useful to discover since it tends to obscure the variation between populations.

(d) Taxonomic Characters

The taxonomic characters employed in this study of *Peromyscus* fall into four groups: pelage, external body measurements, skull measurements, and analysis of blood proteins. Hooper (1958) has found the male phallus to be a useful tool in the taxonomy of *Peromyscus*. An examination of the present material indicates that there is no important difference between the phalli of the two species of mice apart from size which can be more accurately measured on other parts of the animal. Hence the baculum is not included in the present analysis.

Pelage. The pelage in the adult population of mice on the Queen Charlotte Islands is remarkable for its uniformity although, as suggested earlier, a warmer tone in some members might be associated with age. Differences between populations can be detected in some samples. The typical specimen, whether *maniculatus* or *sitkensis* has a distinctly bicolour tail, pale feet, a clear light grey belly, and a slightly darker brown stripe down the middle of the brown back. In one island population the dorsal surface of the feet and body is slightly darker than elsewhere on the Archipelago. More distinctive are the red-brown dots or stripes found on the breasts and bellies of some small island populations. The dots occur as a pair on either side of the mid line just behind the front legs, while the stripes are on either side of the mid line just in front of the hind legs. Both types of mark are found in varying degrees of intensity but all are associated with a greater amount of pigmentation in the rest of the animal: the tail is not so distinctly bicolour, the upper surface of the tarsus of the hind feet is grey, the fur at the base of the hind feet is very dark, black in some, and the belly is a darker grey. This syndrome is of phylogenetic interest in the present study as it occurs, in a greatly intensified form, on the mainland islands directly to the east.

External Body Measurements. In the analysis that follows, body length, tail length and length of hind foot are used.

Skull Measurments. For all complete specimens of *Peromyscus* I made the following measurements: greatest length of cranium, zygomatic width, maxillary tooth row, length of palate, post palate, palatine slits and diastema. These measurements will be analysed in a later section.

Blood Proteins. Serum proteins have been shown to be reasonably conservative among the characteristics of taxonomic importance. Bearing in mind that Bigelow (1958) has pointed out that such conservative characteristics may be convergent, it is worthwhile to examine the serum proteins in relation to the whole spectrum of taxonomic characters. Sibley (1960) gives an excellent review of the application of protein studies to taxonomy. The method has been used by a rapidly growing number of workers: Cowan and Johnson (1962), in deer, Dessauer and Fox (1956), in amphibians and reptiles, and Moody (1958), in muskox. For a number of years, M. L. Johnson of the University of Puget Sound, Tacoma, has been conducting a survey of the serum protein electrophoresis and haemoglobin electrophoresis in a wide assortment of large and small mammals (Johnson and Wicks 1959). These authors have demonstrated apparently species-constant differences.

Specimens of *Peromyscus* were submitted to Johnson from localities on the Queen Charlotte Islands, *sitkensis*: Hotspring I., (5), Ramsay I., (2), and eleven specimens of *keeni* from Sandspit, Moresby I.

> Johnson has returned the following report: "Regarding your *sitkensis* and *keeni*, we have checked around 300 determinations involving 11 other subspecies of *Peromyscus maniculatus* and 10 other species of the genus *Peromyscus*. The intermediate globulins of the genus *Peromyscus* tend to be species specific and *keeni* and *sitkensis* both contain a slow moving globulin which is isoelectric and characteristic of *Peromyscus maniculatus* as shown by the paper technique. Two additional globulin bands are found characteristically and show up well both in *keeni* and *sitkensis*. These might be referred to as number 2 and 3, counting from the point of application towards the albumen with 3 being less readily seen in some cases. The separation of band 1 and 2 shows a very slight difference between *keeni* and the specimens of *sitkensis* that we have examined in that 3 is slightly more distant in *sitkensis*. This, however, is only a suggested difference and with the present techniques is within the realms of variability within the species.
>
> "Therefore, in summary, I would say that *keeni* and *sitkensis*, according to their serum protein electrophoresis and the haemoglobin electrophoresis are conspecific."

(e) The analysis of the samples

The discriminant function:

The most important statistical analysis used in this study of Peromyscus is the discriminant function (Rao 1952) recently used successfully on mice by Delany and Healy (1964). The function is an index which gives a measure of maximum dispersion between samples and using all characters at once. The computing programme was written by D. P. Snyder of the University of Massachusetts in Amherst, using the method of Nash and Jolicoeur (ms.) and is stored in the Computing Centre Library at the University of British Columbia.

The following restrictions are presently placed upon the programme: the maximum number of variates (characters measured) must be equal to 10; the original input data must be scaled so that maximum value of any element is equal to or less than 20; the maximum number of individuals per sample is 25; the maximum number of samples is 35. Since there were at least 55 samples originally, those containing fewer than 10 individuals were generally either dropped from consideration or combined with another from an adjacent location on the same island.

Since some skulls were defective, not all measurements could be taken and these specimens had to be eliminated from the discriminant function analysis since there is no provision for missing data. Similarly those skulls from Age Group 1 were also discarded as the length of the molar tooth row could not be accurately measured.

The following constitute the 35 samples treated by the programme. The number of specimens in the sample is in parenthesis.

1 Hippa I. (20)
2 Gordon I. (12)
3 Frederick I. (16)
4 Anthony I. (11)
5 Kunghit I., Osgood (25)
6 Kunghit I., U.B.C. (9)
7 Marble I. (20)
8 Bischoff I. (8)
9 Bolkus and George I. (19)

10 Hotspring I. (17)
11 Ramsay I. (14)
12 Reef I. (13)
13 Louise I. (17)
14 N. W. Graham I. (12)
15 Rose Spit (15)
16 Skidegate (20)
17 Tasu (14)
18 Cumshewa (13)
19 Harrison I. (13)
20 Chaatl I. (11)
21 Masset (21)
22 Juskatle (17)
23 Queen Charlotte City (13)
24 Harriet and Rose Harbour (18)
25 Peele Inlet and Alpine Lake (14)
26 Sandspit (17)
27 Banks I. (13)
28 Calvert I. (25)
29 Hunter (24)
30 Forrester I. (10)
31 Baranof I. (16)
32 Chichagof I. (11)
33 Admiralty I. (23)
34 Mitkof I. (24)
35 Goose I. (22)

Samples 1 to 26 are from the Queen Charlotte Islands, the first seven of these being from the west coast, the following six from the east coast, while the remaining 13 are from Graham, Moresby and two other closely associated islands. Samples 27, 28, 29 and 35 are from the mainland coast of British Columbia, while the remainder (30 - 34) are from Alaska.

The results of the programme indicated that a logarithmic transformation of the data was not necessary since when the sample mean is plotted against the sample variance no correlation is observable.

Bartlett's Test (Bartlett 1934) was used to test the homogeneity of variance of the samples. The test indicated a high degree of heterogeneity, which could be caused by the wider age spread in some samples than others, or by genetic differences between the populations. Worden (1963) believes that there are so many factors that can contribute to heterogeneity of variance that

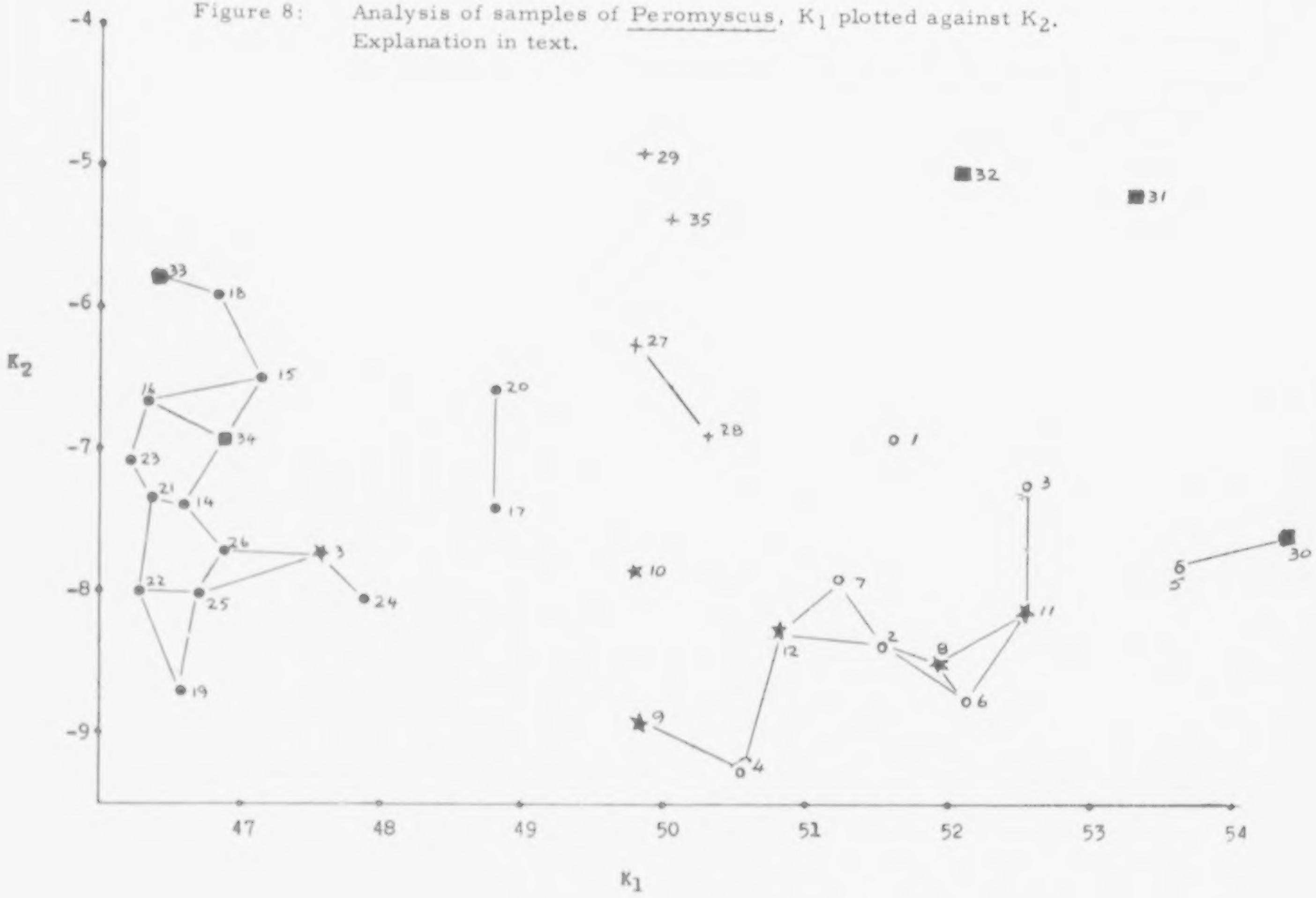


Figure 8: Analysis of samples of Peromyscus, K_1 plotted against K_2. Explanation in text.

the test is not useful. The main consideration is whether the results appear to be meaningful.

Ten discriminant functions (eigenvalues) are calculated and are designated as K_1, K_2, ... K_{10}. These give an indication of the sort of variation present between the samples. The ten eigenvalues, totalled for all samples, are listed in order of decreasing size: 102.97, 20.53, 17.90, 14.28, 9.53, 5.88, 5.43, 4.84, 2.44, and 1.72.

K_1 is much larger than any of the other eigenvalues and consequently most of the differences between populations lie here. Snyder (1963) believes that most of K_1 is due to the fact that size differences between the samples include both "real" differences (genetic or environmental) and those attributable to age. K_2 is likely the result of differences in proportion of the animals, while the remaining eigenvalues reflect unknown differences.

The larger the eigenvalue the more likely is it that it will help to separate the samples and to test this K_1 is plotted against K_2 (Figure 8) for each sample. In the Figure the points represent individual samples, the numbers corresponding to those in the above list. The 13 samples from Graham, Moresby, Chaatl and Harrison Islands (•) include the latter two islands since Chaatle Island is occasionally joined to Moresby at low tide, and Harrison Island is completely and closely enclosed by Graham Island. The samples from the west coast islands of the Queen Charlotte Islands (o) include Kunghit Island. The specimens from this Island have been split into two samples, those collected by Osgood in 1900 and those collected by University of British Columbia expeditions from 1947 to 1961. Islands on the southeast side of the Queen Charlotte Islands (★), four islands along the mainland coast of British Columbia (+), and five islands sampled in Alaska (■), are included in the Figure.

In Figure 8 the points which are joined by a line are not significantly different at the 95% level. The formula for making this calculation may be found in the Appendix.

Figure 8 shows that there are two main groups of *Peromyscus*: those from Graham and Moresby Islands and those from the other islands of the Queen Charlotte Islands. This distinction is not apparent if K_2 is plotted with K_3 since each succeeding eigenvalue has less discriminating power. Eigenvalues beyond K_3 are not useful, the plots using these figures appearing to assort the samples randomly.

The two groups in Figure 8 are primarily separated by the first eigenvalue which is mostly attributed to size differences between the members of samples. Since it has already been shown that samples of *Peromyscus* taken from the outer islands of the Queen Charlotte Islands are substantially older than those from Graham and Moresby Islands, it might be concluded that much of the difference between the two groups is the result of age rather than genetic differences.

During a trial run of the computing programme the adults (9) and subadults (11) of the Hippa Island sample were treated separately; the adult sample had a K_1 value 0.31 larger than the subadult and the K_2 value 0.03 smaller. Neither K_1, K_2 nor their combination is significantly different at the 95% level. It thus appears that while the uneven balance of Age Groups in the different samples may make the results less precise, the broader implications are still valid. Additional evidence to support this view is shown in Figure 8, the sample from Rose Spit (#15) has a high proportion of old mice (73%) yet is not significantly different from the sample from Skidegate (#16) on the same island, which has a high proportion of subadult mice (80%).

Bearing in mind the above limitations, the following are some conclusions which might be derived from the study of the first two eigenvectors in Figure 8. Most of the samples taken on Graham and Moresby Islands are joined by lines and therefore form a group. This is the race of *P. m. keeni*. Some of the samples in the group are significantly different from one another (#22 and #18 for example), but they are not significantly different from other intermediate samples. Hence, while there are clines running through the two islands, only two samples are completely distinct from all others, namely those from Tasu on Moresby Island (#17) and Chaatl Island (#20). These two are not only significantly different from all other samples of *keeni*, but are different in the same way in both being larger (K_1 axis). Each is a semi-isolated population: Tasu is at the end of a peninsula on which the continuity of the forested habitat is greatly restricted by Mt. De La Beche, one of the highest mountains on the islands, and which perhaps significantly lessens gene flow from the mice on the rest of Moresby Island. The Chaatl Island sample is also partially isolated from that on Moresby Island since the two islands are joined by a narrow beach only at the lowest tides. The question whether similarity between these two samples is the result of parallel evolution or because they are from the same genetic stock, is left until the Discussion of this species.

The population on Harrison Island in Juskatla Inlet is isolated by a few hundred yards of water from Graham Island and the sample (#19) indicates a strong affinity with the *keeni* group.

Peromyscus from southern Moresby Island (#24) are the largest on the main islands and this suggests that there has been some interbreeding with a larger form. This theory is given support by the fact that five of 24 specimens from the area have orange belly and/or breast markings, a characteristic which is found in a much more extreme form in the larger race *rubriventer* (#29) found on some of the adjacent mainland islands (Hunter, Bardswell Groups and Smythe Island. See McCabe and Cowan 1945, p. 181). In some specimens from the latter islands the animal's belly is entirely brick red and the colour of the rest of the animal is highly saturated. Less extreme forms are more like those typical of southern Moresby Island. The possibility that there was a direct connection between these two colour groups will be discussed later.

The sample from Louise Island (#13) is the only one from the outer islands of the Queen Charlotte group which is not significantly different from the samples of *keeni*. Upon investigation it has been found that Louise Island is, in fact, joined to Moresby at most low tides, by a short neck of land and intermingling of the populations could, therefore, frequently take place.

P. m. hylaeus is generally considered to be very similar to *keeni* and according to Figure 8, one might conclude that there is no significant difference between the two races. Osgood (1901) writes that there is no appreciable difference between the pelages of the two and that they are best separated on skull characteristics, *keeni* having a heavier skull and shorter, broader, nasals. In the samples under consideration, however, the average length of the nasals on specimens of *hylaeus* from Admiralty Island is actually less than any of the averages of all the samples of *keeni*. The so called "heavier" skulls of *keeni* could be age-dependent and certainly such a character is difficult to quantify. In view of the lack of any clear distinctions between the two races, it is more meaningful to consider that the two names are synonyms, the name *keeni* taking priority over *hylaeus*.

Most of the other points in Figure 8 represent individual small islands. While many of these samples are significantly different from any other, there is one cluster in which nine samples are joined by lines. It is composed entirely of widely spaced samples from the outer islands of the Queen Charlotte Islands and includes the following, listed in order of increasing magnitude of K_1: Blokus-George, Anthony, Reef, Marble, Gordon, Bischoff, Kunghit (UBC), Ramsay, Frederick. Specimens from these islands will be referred to as belonging to the race *prevostensis* in spite of their being somewhat distinct from the type series (#5). The samples from Bolkus-George (#9) and Anthony (#4) contain the smallest individuals in the group and these are further distinguished by possessing the orange breast spots and belly stripes already mentioned. All 47 specimens from Bolkus and George Islands have the breast spots, while 20 have the belly stripes. Eleven of 23 specimens from Anthony Island have the breast spots, three the belly stripes. Specimens from other islands in the immediate area also possess the breast spots and, less frequently, the belly stripes; for example, 10 of 13 specimens from East Copper Island and 11 of 23 from Gordon Island. The belly stripes are never present when the breast spots are absent.

While it is possible that this colour characteristic has arisen separately on each of the six islands, it seems far more likely that it has appeared only once and has since been transported to the other sites. Circumstantial evidence supports the latter view. The Haida Indians had a large encampment at Bella Bella in the heart of the islands which presently supports *rubriventer*. To the west, on the Queen Charlotte Islands, the Haida had camps throughout the area, specifically including Bolkus, Anthony and southern Moresby Island, and it is very likely that the Indians transported *rubriventer* stock to these islands where the mice interbred with the original population to produce a more moderately pigmented form. On those islands of the Queen Charlotte Islands on which this characteristic is most prominent (Bolkus and George), the waifs likely encountered only a small population of *Peromyscus*. It is even possible that *Peromyscus* was entirely absent although this is less creditable, since *rubriventer* (#29) is otherwise distinct from these others with stripes (#2, 4, 9) in the K_2 eigenvalue. In addition, the samples with this characteristic from the Queen Charlotte Islands are not significantly different in Figure 8 from some others from the same region without it (e.g. #12).

It may be observed further that specimens from Kunghit and Rankine Islands fail to show evidence of spots or stripes although both occur in the same region as those which do and in spite of the fact that Kunghit Island had at least three Indian villages on its shores. This suggests that introduction of mice in Indian canoes was not a common occurrence.

The specimens from Bischoff Island (#8) are the darkest of any from the entire Archipelago while not showing any markings on the ventral surface. The skulls show a great range of individual variation, some being almost flat along the top while others are strongly convex. One skull is asymmetrical, having its rostrum pointing distinctly to the left.

The sample collected from Kunghit Island by Osgood in 1900 (#5, the type series of *prevostensis*) was treated separately from specimens collected at least 47 years later (#6). The mice have apparently become significantly smaller in the interim period and a possible reason for this is suggested in the next section. The recently collected topotypes are not significantly different in K_1 and K_2 from eight other islands, all of which will be referred to together as *prevostensis.*

The Hotspring (#10) and Hippa (#1) Island samples are distinct from other samples and one another but are similar to *prevostensis* in size. The Hippa specimens have already been referred to *prevostensis* (Cowan and Guiguet 1956) and it seems that the Hotspring specimens should be as well. It is clear that members of *prevostensis* are far more variable than *keeni* in both size and colour of pelage.

The remaining samples in Figure 8 are from outside the Queen Charlotte Islands. That from Forrester Island (#31) is not significantly different from Osgood's series of *prevostensis* but the race from this island (*P. s. oceanicus*) is distinctively coloured (Cowan 1935). The two samples of *P. m. macrorhinus* (#27, 28) are not significantly different from one another, while the closeness of the samples from Baranof (#31) and Chichagof (#32) support the naming of the two as a distinct race (*P. s. sitkensis*). *P. m. rubriventer* (#29) and *P. m. pluvialis*

(#35) lie close to one another both geographically and in morphologic character as shown in Figure 8, but are readily separable by the intense pigmentation in the former.

P. sitkensis has been generally considered to be a weakly characterized relative of *P. maniculatus* and doubts as to the validity of its taxonomic status have often been expressed (Osgood 1909, Cowan 1935, McCabe and Cowan 1945). Its most outstanding features include large size, large hind feet, short tail and minor skull characteristics including slit-like posterior palatine foramina. Figure 8 indicates that the size of *macrorhinus*, *pluvialis* and *rubriventer* overlaps that of *sitkensis*. The foot size of *sitkensis* overlaps a sample of *maniculatus* from Nigei Island (McCabe and Cowan (*op. cit.*) and while most samples of *sitkensis* do have short tails, some samples such as that from Hibben Island, have long tails (see the next section for details). Slit-like posterior palatine foramina are sometimes found in the samples of *keeni* while round foramina occur in the recently-collected Kunghit Island samples. The electrophoretic patterns of the haemoproteins suggest that the two species are conspecific (Johnson 1963).

In spite of the doubtful distinctions between the two species, there is no overlap of the two in Figure 8, the samples from each always being significantly different from one another. However, some individuals defy classification. In addition, the races within each species are no less distinct from one another than are the two species themselves, and it therefore, seems likely that they are conspecific. All races of *sitkensis* will henceforth be ascribed to *maniculatus*.

Two lines of future research could verify this conclusion: a discriminant function analysis should be done on two well defined species of *Peromyscus* and their races to see whether or not the order of the magnitude separating the species is significantly greater than that separating subspecies. Perhaps even better and more conclusive evidence would be gained by introducing a sample of *maniculatus* to a small island populated with *sitkensis* to determine whether the two interbreed in nature.

Analysis of the Body/Tail Ratios

Almost any of the ten measurements taken on this species could be profitably analysed in detail but the body and tail measurements were chosen since these figures are available for all specimens caught, and their ratio is often diagnostic of different races of Peromyscus. By comparing the ratio of body/tail from one sample to the next, the effect of an uneven sampling of the Age Classes is minimized.

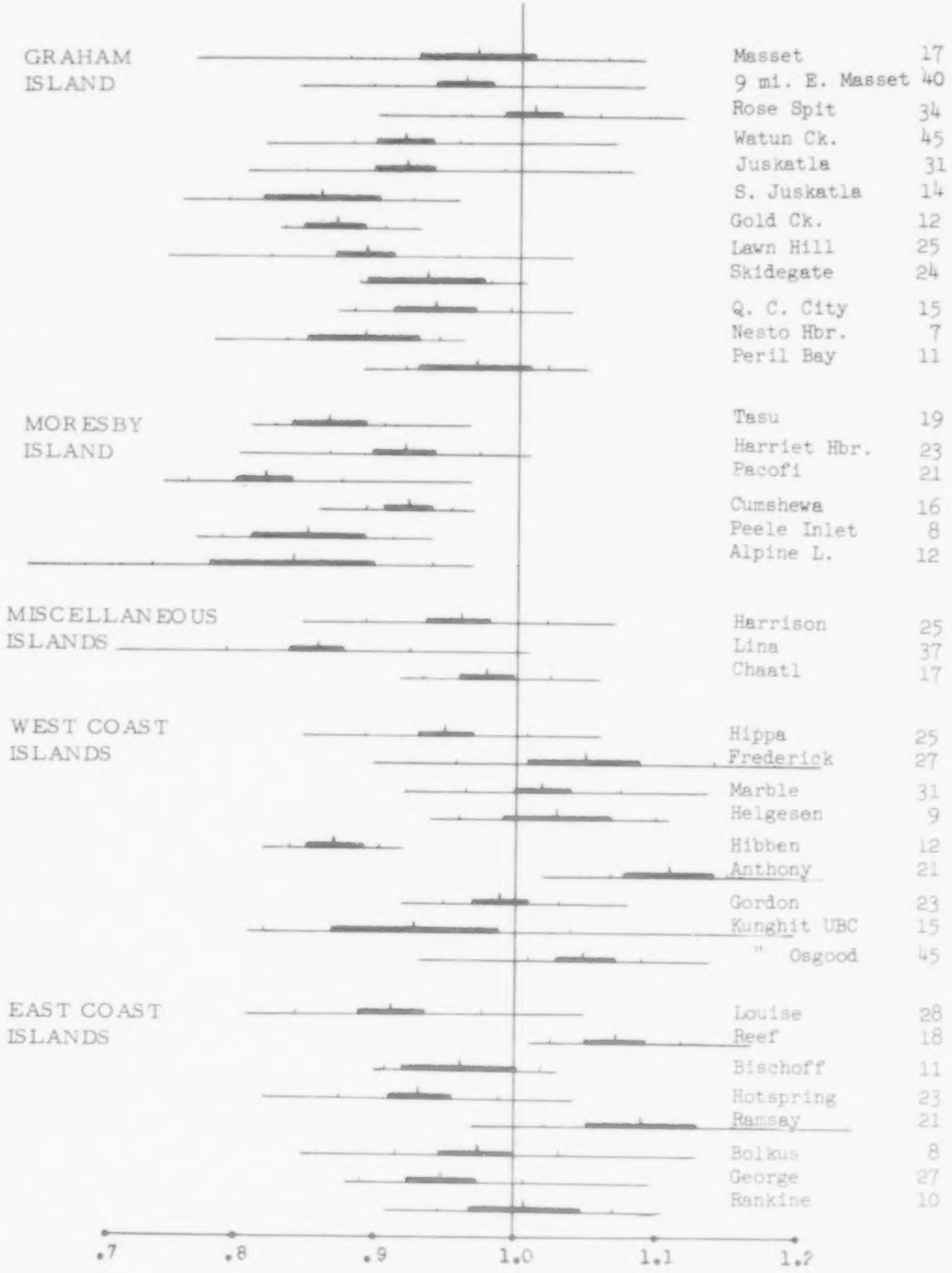
Figure 9 shows the range, mean, two standard deviations and two standard errors (black bar) on either side of the mean for 38 samples of Peromyscus from the Queen Charlotte Islands. The vertical line marks where the body and tail lengths are equal, those to the right of the line having a longer body and those to the left a longer tail.

The total range of variation within Graham and Morseby Island (keeni) compared with that in the outer islands (prevostensis) is approximately equal, although prevostensis does tend to have a proportionately shorter tail. This is not simply a case of allometric growth, since some large mice have long tails (Hibben Island sample) while small mice may have short tails (Rose Spit sample). If the samples from the outer islands are compared with the nearest sample from Graham and Moresby Islands, it may be seen that in 14 of 17 samples the outer island specimens have a significantly higher ratio (proportionately shorter tail). This phenomenon is apparently characteristic of Peromyscus living on small isolated islands since it has already been noted in this species by Hall (1938) and McCabe and Cowan (1945).

An indication of what the evolutionary mechanism might be is given by the two samples from Kunghit Island, one collected in 1900 by Osgood and the others about 50 years later by ourselves. The two populations are significantly different as shown by the eigenvalues in Figure 8 and by the body/tail ratios of Figure 9. The range of variation is very great in the recently collected specimens indicating that perhaps the population is less genetically stable than formerly.

It could be reasoned that the apparent differences between the two samples is actually the consequence of Osgood having used a different measuring technique from that adopted in the present study. However, this explanation is not satisfactory since Osgood also collected samples from Skidegate and Cumshewa which are not greatly different (in Figure 8) from samples recently collected near these localities.

Figure 9: Comparison of body/tail ratios of Peromyscus



In the intervening 50 years one major change has occurred on Kunghit Island: rats (*Rattus r. rattus* and *R. r. alexandrinus*) have been introduced. As outlined earlier, they are present on many of the islands but live together with *Peromyscus* only on those islands which are as large or larger than Kunghit and Lyell Islands; on smaller islands the rat appears to exclude *Peromyscus*. The deer mouse was recently found to be very rare on both Kunghit and Lyell Islands, a condition likely brought about by competition with the rat. On islands without rats, including Kunghit Island in 1900, mice, if present, were abundant.

It is not known how long rats have existed on the Queen Charlotte Islands, although they were absent in 1900 according to Osgood (*op. cit.*). However, it appears that since rats were introduced to Kunghit Island the mice have become not only less abundant but smaller in size (Figure 8), and with a proportionately longer tail (Figure 9). It is suggested that the change is the result of competition with the rat, since by becoming smaller and possessing a longer tail the deer mouse has perhaps become more agile and better able to compete with the large and aggressive rat.

Perhaps the general trend towards shorter tails in *Peromyscus* on the smaller, more isolated islands is the result of there being fewer competitors and/or predators in such typically impoverished environments. However, this theory does not explain the great range of body/tail ratios on many of the islands. Specimens from rat-free Hibben Island, for example, have long tails and yet no competitors or predators are known on this island which would confer an advantage on long tails. A detailed study of the ecology of the species on each island would be necessary before particular examples could be understood.

(f) Discussion

An adequate assessment of the evolution of *Peromyscus* on the Queen Charlotte Islands must take into account many variables. These include gene flow, as, for example, that aided by Indian canoes, the effect on the populations of different degrees of isolation in both space and time, genetic drift, and the effect of ecological factors such as interspecific and intraspecific competition within each population. These variables, all operating at once, make it impossible to arrive at any conclusion with certainty.

The distribution of the forms of *Peromyscus* in the region clearly parallels that of the shrew. In both groups a small form is found on Graham and Moresby Islands and some of the islands of the Alexander Archipelago, while larger forms are found on Kunghit Island and some of the other outer islands of the Queen Charlotte Islands. The larger forms have their closest relatives on the adjacent mainland. Ideally the same theory would satisfy the evidence from both species but, unfortunately, the problem of the distribution of *Peromyscus* in the region is considerably more complicated due to the greater number of islands sampled and the fact that it is a more plastic species.

As pointed out earlier two theories have been put forward to explain such distributions: in the first it is suggested that they are the result of the combination of original inhabitants (relicts) and more recent competitive invaders; while the second holds that all forms have evolved on the islands from a common ancestor. Cowan (1935) invokes the former theory to explain the distribution of *maniculatus* and *sitkensis* in the region, while Steven (1953), Corbet (1961) and Cook (1961) support the latter for a similar situation in Britain.

> Cowan writes, (*op. cit.*, p. 429) "The range of this species (*sitkensis*), confined as it is to the outermost chain of islands or islets of the Alaskan and British Columbian coast, might be explained by supposing that the species is a relatively old one which was able to persist on the outermost islands while the adjoining mainland and inner islands were undergoing Pleistocene glaciation. The inner islands and the mainland are now colonized by the smaller *Peromyscus maniculatus*, and *P. sitkensis* always occurs alone: these facts suggest that *sitkensis* possesses adaptability inferior to that of *maniculatus* and therefore cannot survive in active competition with it."

The evidence presented earlier indicates that the only likely refugium in the region was on the Queen Charlotte Islands and that *Peromyscus* might have been able to survive there. However, samples collected since 1935 have shown that the two "species" do, in fact, form a cline in size (K_1 eigenvalue) and most other characteristics. If this is the result of recent and common lineage, the relict hypothesis is not valid. Perhaps either the large mice of the mainland (*macrorhinus* for example) have populated the outer islands of the Queen Charlotte Islands and Alaska, or vice-versa. The former would be more likely since rarely are island stocks successful when introduced to the mainland (Seton's Law). Alternatively, perhaps the similarity of *sitkensis* to *macrorhinus* is the result of parallel development in which case all the large insular mice could be explained in this way.

The fact that the two "species" always exist alone could be either for the reason given by Cowan, or because there is interbreeding at any time that the two come together. According to the latter reasoning, if an island is not populated with either form and is invaded by one, the waif becomes established; on the other hand, if either form is present, the waifs are absorbed into the population conferring little new genetic variability to it unless the island is small or the population at a low level.

The relict theory has as a corollary that few of the smaller, more efficient mice, would be needed to eventually displace the larger from an island. There is good reason to believe that Haida canoes occasionally transported waifs to most islands thereby giving abundant opportunity for such a displacement to have occurred. Since it has not happened, I propose that it is because the two interbreed.

There is no direct evidence that *sitkensis* cannot survive active competition with *maniculatus*, while the similarity of the two suggests that interbreeding would be possible. Clearly, the solution to this problem lies in introducing a sample of *maniculatus* to an island populated with *sitkensis* and observing whether interbreeding or dominance by *maniculatus* occurs. In the analagous situation in Britain, Steven (1953) was able to breed the insular and mainland form of *Clethrionomys*, and uses this as evidence against the relict hypothesis.

Cowan (*op. cit.*) continues, "If it be assumed that within *sitkensis* the populations of these small islands have been isolated from one another, it is not unreasonable that each should exhibit certain distinctive characters both of colour and of proportions of body and cranium."

It has already been shown (Figure 8) that the differences which separate some of the races of "*P. sitkensis*" are considerable. It is difficult to say how great these differences must be before the theory of common origin becomes suspect and the theory of parallel evolution towards large size is invoked. It is the presence of such superficial resemblance among some of the mammals living on islets in Britain which convinces Cook (*op. cit.*) of the invalidity of the relict story.

The second theory contends that all the forms have descended from a common ancestor since the retreat of the glaciers, either from a population which existed in the Charlotte refugia or from early arrivals from the mainland.

Had *Peromyscus* lived in isolation in the refugia for some 100,000 years, one would now expect the animal to be distinct. However, *prevostensis* is similar to *macrorhinus* and *keeni* to *P. m. oreas* (Osgood 1909) and consequently a long tenure in a refugium seems unnecessary.

P. macrorhinus is now widely spread along the mainland coast and it would thus seem arguable that its ancestors were the first to reach the Queen Charlotte Islands, where, in due course, they would have spread over most of the islands giving rise to *keeni* and *prevostensis*. This explanation seems untenable since evolution tends to proceed more quickly in small, isolated populations, yet *keeni* is more dissimilar to *macrorhinus* than is *prevostensis*.

A more plausible explanation is that a form similar to *keeni* moved up the coast from the Washington refugium as the glaciers retreated and colonized most of the Queen Charlotte Islands and the Alexander Archipelago. In the interim slight differences had appeared in populations on most of the large islands and it became what is now known as *keeni*, while on the smaller isolated or semi-isolated populations of the Queen Charlotte Islands, Alaska and the mainland coast to morphologic differences became considerably greater, particularly with regard to the large size. According to this theory, the similarity of all the large forms in the area is the result of parallel evolution and it holds that some characteristic or characteristics of small, isolated, or semi-isolated populations selects the larger forms. The possible mechanism involved will be discussed after the completion of a wider survey of insular races of mammals in the following section.

While the members of the small insular population are uniformly large, this character varies greatly in degree (K_1 eigenvalue) and generally the members are less conservative than are the smaller mice. Occasionally mutants have been successful in producing striking changes other than size, for example, in the specimens of rubriventer, those from Bischoff Island, or the occasional melanistic forms found on Frederick Island.

It is certain that Indian canoes have played a role in the spread of mice throughout the area and some islands have likely had multiple introductions. However, the importance of the part played by such gene flow in aiding or retarding evolutionary trends is unknown.

Since, in general, the small isolated islands have large mice and the large islands small, it is essential to account for the fact that the large race sitkensis is found living on the large islands of Baranof and Chichagof. It appears that large size is evolved only in small, isolated populations, and consequently it is suggested that Baranof and Chichagof Islands were first populated by waifs which were already large, having become so on some adjacent small island. Keeni failed to reach these islands first perhaps because the surrounding deep water channels would have prevented any postglacial land-bridge from forming.

Another reason for the apparent breakdown in inverse relationship between island size and size of mouse could be because the overall size of the island is less important a factor in rapid evolution than is the size of the population living on the island. To determine this for each island would involve a far more lengthy study than reported herein.

P. macrorhinus is partly distributed on the mainland and yet it is of large size. This could be for at least three reasons. Firstly, most of the collecting has been done on the headlands many of which could be populated with almost as completely isolated populations as that at Tasu. Secondly, rubriventer characters are found in a less extreme form on some of the headlands, and it is apparent that some of these large mice have been taken there from the islands. Thirdly, McCabe and Cowan (1945, p. 202) write that the high postglacial shoreline would have transferred many of the present headlands into small islands thereby providing the requirements for evolution towards large size. The extreme ruggedness of the terrain permits these "insular" forms to remain distinct.

(g) Summary and conclusions

The discriminant function analysis is a useful tool to compare samples of *Peromyscus*. Samples collected within a few miles of one another on the same island (#16 and #23, for example) are shown to be close to one another in the analysis (Figure 8), while, on the other hand, animals which have always been considered to be very distinct (the type localities for *keeni* #21 and *prevostensis* #5) are widely spaced in the graph. The work of earlier taxonomists who did not have access to the discriminant function is usually verified in the present analysis. For example, Cowan (1935) considers that *sitkensis* from Chichagof Island is noticeably smaller than those from Baranof Island, that *oceanicus* is more like *prevostensis* than *P. s. sitkensis*, and Osgood (1909) writes that *macrorhinus* is most like *sitkensis*. These conclusions are verified by the method used in the present survey. However, other relationships were discovered which were not foreseen.

The evidence presented indicates that there is no significant difference between *keeni* and *hylaeus* and that henceforth the range of *keeni* is considered to extend from Graham and Moresby Island at least as far north as Admiralty Island. Even though *keeni* extends over this great range, members of the race are not nearly as variable as those referred to *prevostensis.*

The status of the species *sitkensis* has been in doubt for a long time and the present analysis indicates that it is conspecific with *maniculatus.*

It is unlikely that the evolutionary history of *Peromyscus* in the region will ever be directly apparent, due to the slim chance of finding fossil evidence. Only the two most commonly proposed theories have been analysed, though it is realized that there are very many more complicated explanations.

The relict hypothesis is shown to be unsatisfactory due to the apparent integration between the two size groups and the great range of variability found in the "relict" form. The second hypothesis has been modified to include multiple invasions and is summarized diagrammatically in Figure 10. The most important assumption in this hypothesis is that a small

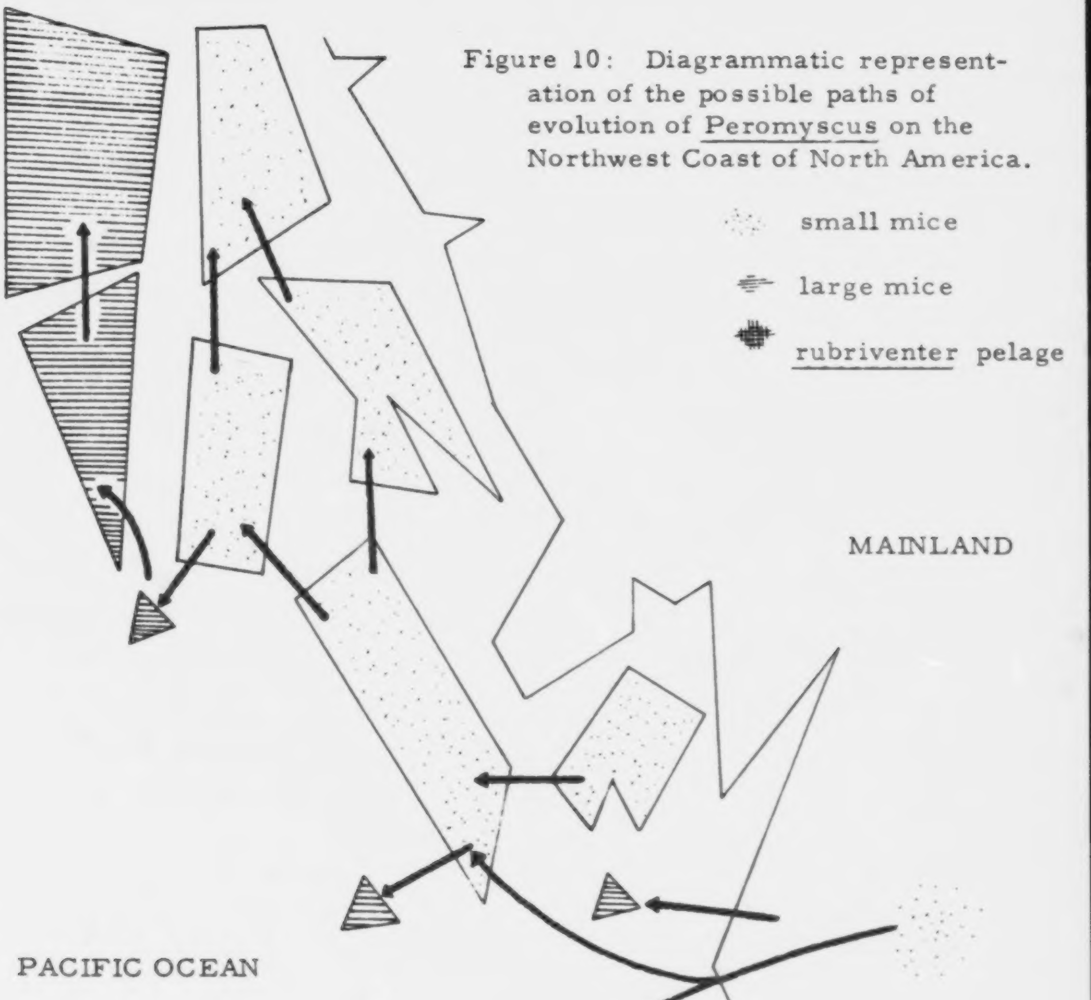


Figure 10: Diagrammatic representation of the possible paths of evolution of *Peromyscus* on the Northwest Coast of North America.

small mice
large mice
rubriventer pelage
MAINLAND
PACIFIC OCEAN

form similar to keeni lived on the mainland immediately after glaciation and gave rise to all the forms in the area. The mice became larger and frequently developed shorter tails when they had been isolated on a small island for a sufficient length of time. Occasionally these mice were transported to uninhabited large islands and remained large in size.

It has been shown that mice living on isolated islands tend to live longer than those elsewhere. According to Rensch (1959) this could be because larger forms within a group usually live longer.

CONCLUSION

This section has outlined some of the possible paths of evolution of the native Charlotte mammals. Evidence indicates that the weasel, bear, marten and *S. o. elassodon* might have lived in the Charlotte refugia, while the otter, caribou, *S. o. prevostensis* and deer mice perhaps did not. Their characteristics apparently evolved in isolation on the Islands and are not the consequence of the animals being relicts. Before the evolutionary forces which might have determined the characteristics are discussed in detail, a wide survey of insular mammals will be made in order to ascertain whether morphological trends are discernible in such populations.

THE EVOLUTION OF MAMMALS ON OTHER ISLANDS

INTRODUCTION

There is a wealth of other islands throughout the world from which one might hope to find evidence concerning the characteristics of mammals living on isolated islands. It should be possible to compare the subspecies of a species on an island with the nearest subspecies of the same species on the adjacent mainland. In the case of an endemic species on an island it is usually possible to compare it with the closest relative of the same genus on the mainland. However, if there are many species of the genus on the adjacent mainland it may prove difficult, or impossible, to know which to select for comparison with the island form. The problem becomes acute when the island form belongs to an endemic genus, as frequently occurs on oceanic islands and occasionally on the more isolated continental islands such as those in Malaysia. As a result these islands will be excluded from the survey; only where close relationship is beyond reasonable doubt, as in the races of a species, will reference be made to them. In this discussion I will assume that the mainland forms have given rise to those found on the island, and that the latter are not relicts.

In comparing the published description of a form of insular mammal with its presumed progenitor on the mainland there is abundant opportunity for error. For example, in many cases the age of the individuals is not stated so it is conceivable that subadults in one population might be compared with the larger adults of another. As shown earlier, older specimens of *Peromyscus* have a body length up to ten per cent longer than subadult. Measurements are often taken by different collectors and could introduce error. Although many authors have examined dozens of specimens, they have usually only published the mean measurements of 10 or fewer. Not only could such small numbers introduce error, but the selection by the author might be biased. Some descriptions only state "bigger" or "smaller" with no reference to how much bigger or smaller, and without stating the size of the samples used. Finally, in comparing island stocks with those from the adjacent mainland, it is possible that the apparent ancestral mainland stock is not the actual one, the true ancestors having emigrated from the area next to the island, or become extinct.

In spite of these potential sources for error, I believe that general size trends should be detected, if present.

MATERIAL AND METHODS

The islands which proved most useful in the survey include those in western North America north from the Panama Canal to the Bering Sea, and include the islands off the coast of Baja, California, Los Angeles, British Columbia and Alaska. From these there is quantitative information. Qualitative data are readily obtained from Europe. While an extensive search of the literature could no doubt have produced further examples from other islands, I believe that the sample of 120 island comparisons, additional to those from the Queen Charlotte Islands is adequate to show any trends which may be present in insular mammals. For details of the individual comparisons see Foster (1963).

The data were gathered from the following sources: British Columbia Peromyscus, Cowan and Guiguet (1956); other North American mammals, Hall and Kelson (1959) and references cited therein; European mammals, Miller (1912).

RESULTS

Table 2 lists the results for each order of mammals considered. There appears to be a tendency for large mammals to become smaller, and small larger, on islands. Details of the trend in rodents are shown in Fig. 11.

Figure 11 indicates that British Columbian Peromyscus (excluding the Queen Charlotte Islands) show the greatest increase in body size. They average 14% larger while those from California and Mexico average 8%. This difference is significant at the 95% level of significance (t = 2.73).

The body/tail ratio were also examined for the samples of Peromyscus. The significance of these differences is shown in Figure 12. Those mainland forms with a body/tail ratio of less than one have their tails longer than the body. All members of this group except one, P. m. madrensis, have shorter tails when represented on the nearby islands. But when, in the mainland form, the tail is shorter than the body, the tail on the island form may become proportionately shorter or longer. In other words, insular Peromyscus have proportionately shorter tails

Figure 11: Size of body of insular rodents compared with relatives on the adjacent island.

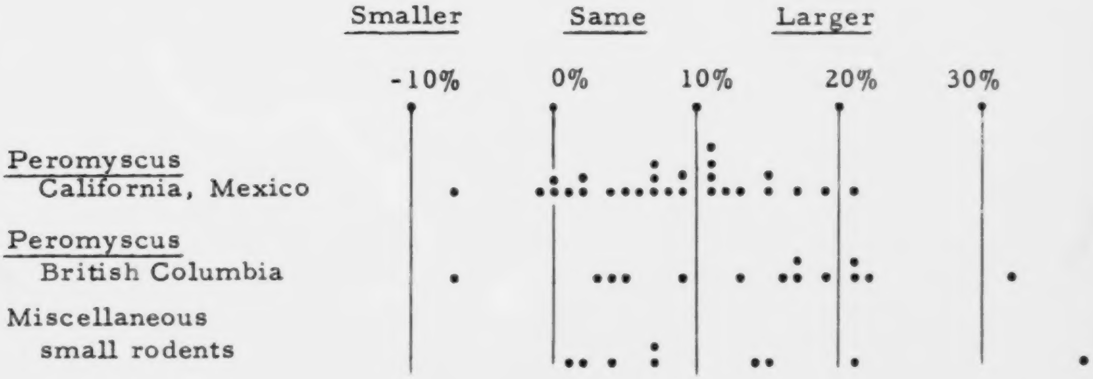
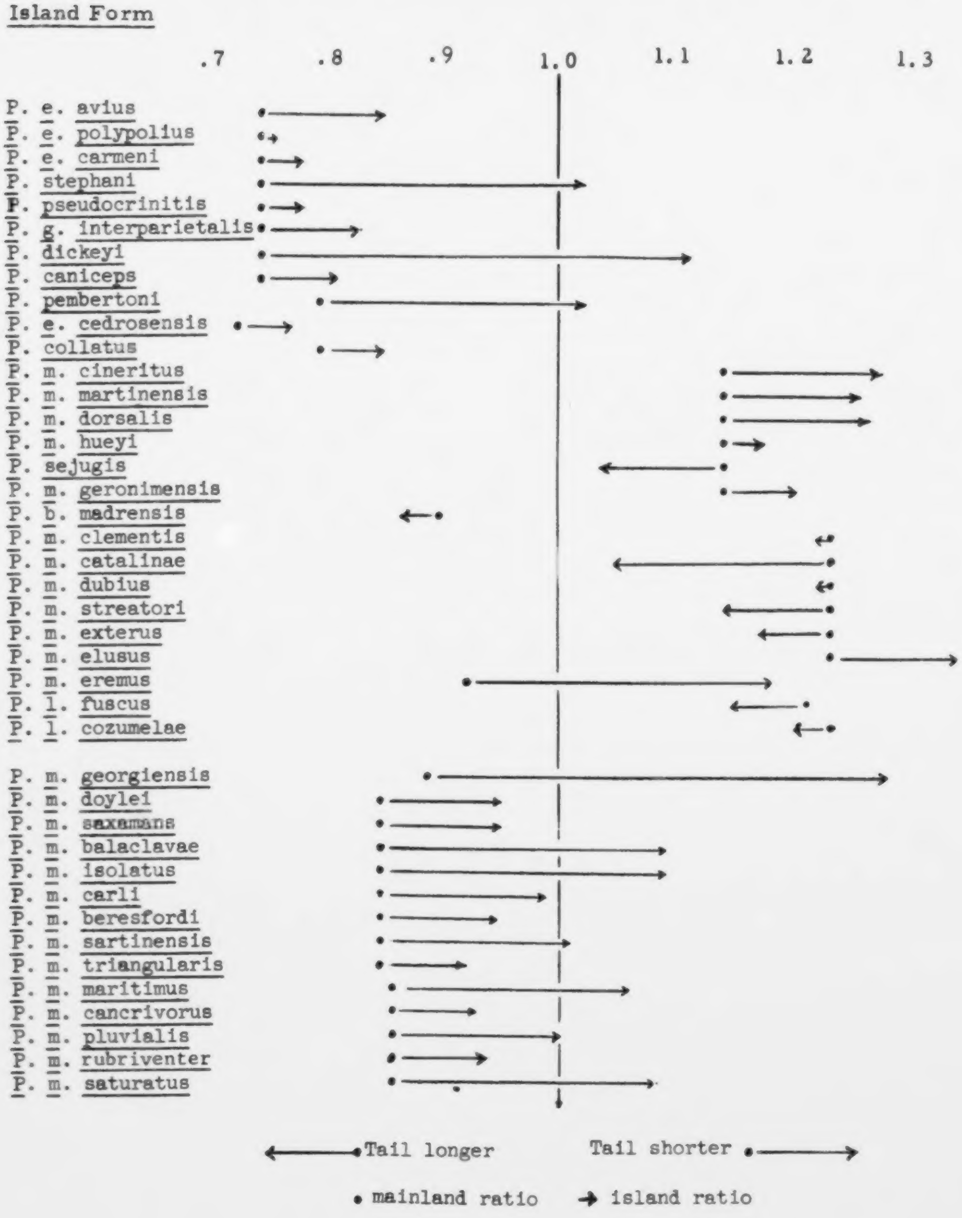


Table 2

Size of insular mammals compared with relatives on the adjacent mainland and excluding those from the Queen Charlotte Islands.

	Smaller	Same	Larger
Marsupials	0	1	3
Insectivores	4	4	1
Lagomorphs	6	1	1
Rodents	6	3	60
Carnivores	13	1	1
Artiodactyls	9	2	0

Figure 12: Body/tail ratio of insular Peromyscus compared with relatives on the adjacent mainland.



than those on the nearby mainland, only if the mainland form has a tail longer than the body. The net result is that either island forms have the tail shorter than the body, or appear to have been evolving in that direction. The fact that not all large mice have short tails indicates that the change in tail length is unlikely to be an example of allometric growth.

DISCUSSION

For an outline of statements in the literature, regarding the size of vertebrates on Islands see Foster (1963). Concerning mammals, Hesse, Allee and Schmidt (1951, p. 62B) give the most comprehensive coverage, but it is confusing since they point out that small mammals may exhibit larger average size on islands, yet "the dwarfing of both mammals and birds is a peculiarity of insular faunae."

Their account is confusing since they have considered the whole class at once. This error is repeated by other workers (Banfield 1963, Simpson 1953, Hantzsch 105). By breaking the class into orders I have shown that there is a clear tendency towards giantism in small rodents and perhaps marsupials. Dwarfism is characteristic of insular lagomorphs, carnivores and artiodactyls. For others the evidence is inconclusive.

The tendency for insular Peromyscus to have a proportionately shorter tail than do the forms on the mainland is now established. A thorough study of the exceptions to the body and tail length trends could be revealing.

A discussion of the possible reasons behind the development of insular characteristics in different mammal groups is left until the final section.

In the foregoing discussion I have assumed that the change in size of island forms is due to an insular environment and that they are not relicts. It is now necessary to attempt to substantiate this supposition. The controversy in Europe concerning Clethrionomys has already been mentioned. Steven (1953), Corbet (1963), and Cook (1961) consider insular development to be more likely than the relict hypothesis since the island mice are similar only in their large size, differing in coat colour, tooth pattern and tail length. Had they been relicts of the same original population they would have expected the island mice to be similar in almost every respect. However, since one would expect some differences between island populations derived from a common stock, due to conditions peculiar to islands in general (perhaps genetic drift), and the islands in particular, this explanation is not entirely satisfactory. The two theories are not mutually exclusive since relict populations on islands are likely to evolve to some extent. The problem is to decide how much difference must there be between relict populations supposedly derived from the same stock before one rejects the relict hypothesis and accepts that the differences are entirely an insular development. Similarities, such as the large body size of insular rodents, could be attributed to parallel evolution.

In North America data are most complete for *Peromyscus maniculatus.* The body length of the mainland forms lie within a small range from south to north (Osgood 1909): Baja California (*coolodgei*), 89mm., Berkeley (*gambeli*), 89 mm., Oregon (*rubidus*), 97 mm., Rivers Inlet (*oreas*), 95 mm., and Pitt Island (*macrorhinus*), 104 mm. Over a span of 2000 miles latitude the body length varies only from about 89 mm. to 97 mm. excluding *macrorhinus*, which race is partly insular thus perhaps accounting for its larger size. *P. m. arcticus* from Ft. Simpson has a body length of about 95 mm.

Over the same latitude island forms of *Peromyscus maniculatus* vary in body length from 88 mm. (Santa Cruz Island, Mexico), to 118 mm. (Sartine Island, B. C.). This range (30 mm.) is considerably greater than that found on the adjacent mainland (18 mm. if *macrorhinus* is excluded). While one can postulate that at the time of colonization of the islands the mainland forms were larger, there is no convincing evidence for this. If their larger size were due to adaption to the cooler environment of the Pleistocene, would this effect have been felt as far south as Mexico? Perhaps they were large because they were at the edge of their range (Salt 1962). On the other hand, *P. m. arcticus* living in a cold environment at the edge of its range has a body length of only average dimensions for the species. I believe it is far more likely that these small rodents have developed their large size as a result of lengthy isolation.

Degree of isolation and body size

South of the region formerly covered by the Pleistocene ice sheet it is usually very difficult to place an approximate age on individual islands. Certainly it is impossible to know when a particular species colonized an island since it very likely happened more than once during a span of time much greater than available to glaciated islands.

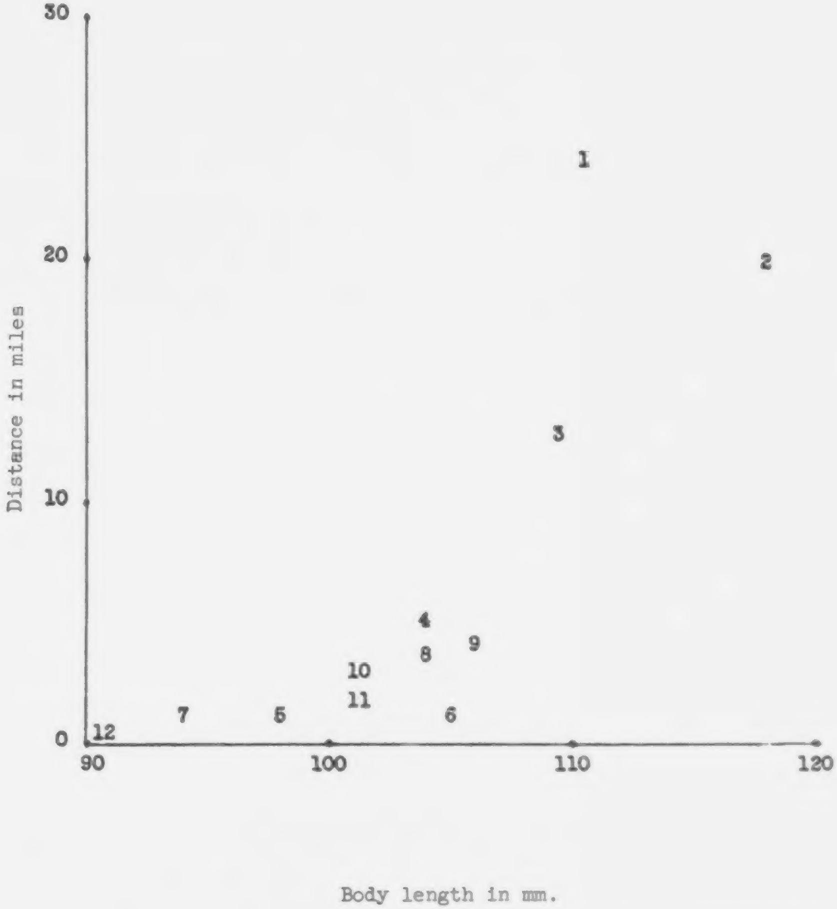
In the Adriatic a large number of islands have been formed by the subsidence of the land since the end of the Pleistocene. The age of the islands may be approximated by calculating the present water depth separating them. Many are inhabited by distinctive races of lizards. Kramer and Mertens (1938) show that the smaller the island, the smaller the lizard population, and the more different it has become from the ancestral mainland types. They show also that the older islands tend to contain more endemic forms. Presumably the authors consider the possibility of "rafting" to be minimal.

In British Columbia, it is safe to conclude that most of the islands became ice free about 10,000 years ago (Matthews 1962) and that most of their mouse populations are of about the same age. There remain two variable factors, either of which might be correlated with change in body size: degree of isolation of the island, and the size of the island. With respect to the former it is necessary to determine the most likely source of waifs. Sometimes it is impossible to know which of two sources for the transplant is more likely as, for example, with Pine Island and some of the islands in the Strait of Georgia. In addition, a short but turbulent water barrier may be as effective as a wide, placid one.

In spite of these difficulties, when body length is plotted against the number of miles from the island to the likeliest source of animals, a trend is observed (Figure 13). (Body measurements are taken from Cowan and Guiguet (1956).) Those animals with the greatest body length tend to come from the islands which are most isolated. There are several possible explanations for this phenomenon. Perhaps the sample is too small since there are only three islands further than six miles from the mainland. All three are in the Scott Island Group and the large size of the mice on these islands could be the result of dispersion within the group although this is unlikely since log rafts and Indian canoes would far more likely originate on the mainland.

The relationship would be more convincing if there were a second instance of its occurrence. Ideally one looks for an island chain extending out from the mainland into the ocean, and supporting endemic races of rodents. Island chains are

Figure 13: Comparison of average body size of insular *Peromyscus* in British Columbia with the distance to the most likely origin of the population.



1. *P. m. triangularis*
2. *P. m. sartinensis*
3. *P. m. beresfordi*
4. *P. m. carli*
5. *P. m. balaclavae*
6. *P. m. saximanus*
7. *P. m. cancrivorus*
8. *P. m. pluvialis*
9. *P. m. maritimus*
10. *P. m. georgiensis*
11. *P. m. saturatus*
12. *P. m. interdictus*

not uncommon, the Aleutians and the Florida Keys being two good examples, but unless a series of insular races is found in the chain, it is difficult to obtain comparative measurements for each population. There are no endemic rodents on the Keys. However, in the Aleutians there are two races of the collared lemming, *Dicrostonyx groenlandicus stevensoni* on Umnak Island, and *unalascensis* on Unalaska Island. Unimak, Unalaska and Umnak Islands are part of the chain of islands which extend towards the west from the mainland. Umnak Island and its race *stevensoni* is the most isolated, with *unalascensis* closer to the mainland; *stevensoni* is the largest race of lemming in North America being larger than *unalascenis* which in turn is larger than the mainland form (Nelson 1929). This is thus a second example of a correlation between degree of isolation and body size.

Perhaps the largest mice occur on the most distant islands because of the insular climate. In temperate climates, islands far out to sea would have a more severe climate, to a human at least, than an island which is partially protected. As a result of the weather there could be a stronger selection for large size on the outer islands. Until information is available on the microclimate of these islands, this theory is only conjecture.

Another explanation considers that on the more distant islands, gene flow to the neighbouring islands or mainland would be minimal, those islands separated by a few miles or less standing a greater chance of acquiring waifs by log rafts or Indian canoes. Perhaps repeated innoculations in such a manner could prevent the animals on these islands from becoming as large as those of the more isolated populations. The discussion of the effect of gene flow in such a situation will be left until the final section.

If the body length of insular *Peromyscus* does, in fact, vary with the degree of isolation, one might expect tail length to do so as well. Hall (1938) claims that this is true for *Peromyscus* living on some of the islands in Georgia Strait. On five of six islands he shows that the tail length varies inversely as the distance to the mainland. Hall's example is inconclusive since some of the islands are closer to Vancouver Island than to the mainland and because of its size, Vancouver Island could equally well act as a "mainland". Consequently the following examples are taken from an area where the likely source for the waifs is less questionable. The insular forms examined are those which are shown in Figure 13. All these island forms have tails proportionately shorter than do those of the "mainland" although within the islands there is no regular change with greater isolation. This could be because some islands are perhaps more rugged, necessitating more climbing and therefore favouring a longer tail for balance. However, until a more detailed study is made of the ecology of *Peromyscus* on each island, such a theory is only speculation.

Since, as a rule, only small islands are populated with large mice, there is probably an inverse relation between degree of evolutionary change and size of gene pool.

SUMMARY AND CONCLUSIONS

As a result of a survey of 120 forms of insular mammals it is apparent that some groups tend to have larger body size (rodents, and perhaps marsupials), while others tend to be smaller than adjacent mainland representatives (artiodactyls, lagomorphs, carnivores, and perhaps insectivores). Members of the genus *Peromyscus* generally have shorter tails on islands. The fact that there are these trends within groups is taken as evidence that the forms are not relicts, but arise as a result of the insular conditions.

The greater range of variation of insular *Peromyscus* when compared with the population on the nearby mainland is further evidence of the effect of the insular environment. Evidence suggests that both the island size, (i.e. gene pool size), and its degree of isolation, have had important effects on the insular form.

DISCUSSION

Within some groups of mammals members of isolated populations possess morphologic characteristics which differentiates them from relatives living on the nearby mainland. In the foregoing section a considerable body of evidence has been assembled to suggest that these differences, in some cases, tend to be uniform in type and reflect similar responses to the insular environment. Whether these island forms are relicts or whether they have acquired their similar insular characteristics *in situ* as a result of parallel evolution, cannot be ascertained with absolute certainty until the discovery of fossil material on the mainland which is unquestionably consubspecific with relicts. Less conclusive evidence in support of the insular evolution of the characteristics has been recorded in many of the earlier sections and may be summarized here under four headings.

Firstly, it has been found in the present study of *Peromyscus* living on the Queen Charlotte Islands that the differences between the small island "relict" populations are greater than one would expect had they owed their similarity to a common origin. Steven (1953), Delany and Bishop (1960), Corbet (1963), and Cook (1961) evoke the same argument to refute the relict concept for *Clethrionomys* living on the small islands of Great Britain. The conclusion is subject to dispute since one would expect such small, isolated, populations to be somewhat distinct even if they were relicts. In *Peromyscus* the form on small islands is considerably more varied in colour, size and proportions than are the populations which belong to one gene pool distributed over an equally large range, and this tendency has been shown by other workers (Mayr 1954, Dobzhansky 1957). It is evident that the insular environment has had a significant effect on the animals.

Secondly, the original relict concept, as stated by Barrett-Hamilton and Hinton (1914) for mammals in Great Britain, and Cowan (1935) for British Columbia, contains, as an integral part, the argument that the smaller mouse dominates the larger and has displaced it from most of its original range leaving it as a relict. There is no direct evidence that such a displacement has occurred and there is an increasing body of evidence to suggest that it did not. Steven (*op. cit.*) has been able to breed successfully the two sizes of mice studied by Barrett-Hamilton and Hinton, and indirect evidence indicates that this should be possible for "*P. sitkensis*" and *P. maniculatus.* Hence, rather than displacement of one form by the other the two might be more likely to interbreed should they come in contact with one another. The displacement theory also presupposes that very few of the small mice would be needed in a waif introduction to eventually displace the larger forms. The evidence is strong that such introductions occurred within the Queen Charlotte Islands when the Indians were active and consequently there would have been an opportunity on most of the small islands for *keeni* to have displaced *prevostensis.*

Thirdly, the fact that different species of insular birds and mammals often tend to be uniformly different from presumed ancestors on the adjacent mainland is evidence that the difference is likely the consequence of insularity. The alternative is to reason, for example, that most forms of rodents, over a wide geographical area and space of time, were larger when the islands first became occupied, that deer were smaller, and so on. There is no evidence to support this alternative.

Finally, the relict hypothesis necessitates the argument that large size is a conservative character (Cook 1961), whereas there is evidence that it may be quite the opposite (Cope 1886, Newell 1949, Mayr 1952, Darlington 1959, Simpson 1953, p. 151, Rensch 1959, p. 211).

Mayr (1952) summarizes his opinion of the relict hypothesis when he comments upon Zimmerman's (1950) paper, wherein the theory is used to explain the parallel situation of large and small *Clethrionomys* (voles) in Britain and Europe:

> "The selective situation does not seem to have been sufficiently considered in this and similar studies. If in a warm period a large-sized population on the mainland is replaced by a small-sized one, this does not necessarily prove a changing population by migration. The change in size could as well be due to a genetic alteration of the mainland population as a consequence of selection pressure. The large-sized island population might be explained as adaptive. Much that is known about morphological changes in recently isolated mammal populations contradicts the notion that size is a conservative character. The fact that neighbouring islands are frequently occupied by populations

with very different phenotypes also indicates rapidity of morphological change."

There is no evidence that the bear, marten, weasel or caribou of the Queen Charlotte Islands owe their distinctive characteristics to their being relict populations and until evidence to the contrary is discovered, it can be assumed that they, too, evolved these features as a result of lengthy isolation. In the case of the shrew, it is thought that two stocks arepresent but there is no evidence that either is a geographical relict.

It has been shown that rates of evolution cover a wide range and some are sufficiently rapid for all the endemic races of birds and mammals on the Queen Charlotte Islands to have appeared in the last 10,000 years. However, within a given group under similar conditions the evolution rate tends to vary within narrow limits (Simpson 1961). Consequently the distinctive characteristics of the Charlotte bear, marten, weasel and *S. o. elassodon* compared with their nearby relatives suggests a longer tenure in isolation, perhaps in the Charlotte refugia for the extent of the Vashon glaciation. Factors affecting this conclusion, especially as relating to rates of evolution, have been discussed earlier.

Some of the above theories could be readily tested. If a few specimens of *maniculatus* were introduced to a small island populated with *sitkensis* it should be possible to see whether they interbreed. Further, by introducing a small form of mainland mouse to an unpopulated small island, it should be possible to see whether evolution takes place rapidly in the direction of larger size and shorter tail. Guiguet (1962) began such an experiment 12 years ago on small islands near Victoria, British Columbia, and it appears that the island forms are already somewhat larger than the original stock. Upon investigation I found that these differences can mostly, if not entirely, be attributed to the old age of most of the specimens, an insular characteristic in itself. However, Steven (1953) suggests that a significant size increase might be discernible within the life span of man.

It has been possible, in the course of this study, to determine similar characteristics in different insular species and it now remains to speculate as to the underlying evolutionary processes.

The most universal trend is that concerned with general body size. The widest generalization which can be proposed from the data (Table 2) is that mammals smaller than rabbits tend to be larger on islands, while mammals of rabbit-size and larger tend to be smaller. The exceptions to these rules are the rabbit-size marsupials which show a tendency to be larger on islands and the small insectivores which sometimes tend to be smaller. For the other four orders studied (carnivores, artiodactyls, rodents and lagomorphs) these rules seem to hold.

Because the different kinds of size characteristics of insular mammals have not been well recognized until now there are no theories published which could account for all the trends which have been described. Thus Hesse, Allee and Schmidt (1951, p. 630) write "The dwarfing of both mammals and birds is a peculiarity of insular fauna, probably referrable to correlation with limitation of space." However, Godfrey (1958) writes, "Size is probably correlated with the ability to escape particular predators, and the relative frequency of these does vary geographically." Bergman (1847) perhaps would reason that some of the differences could be due to differences in the mean air temperature, while Krumbiegel (1943) would postulate that small insular mammals could be the result of inbreeding.

For an analysis of the problem, groups whose members become larger on islands must be separated from those which become smaller (see Table 2). Considering first the artiodactyls as examples of the latter, it is likely that their small size is caused by the lack of predators on the islands and the limited food supplies resulting in malnutrition; that the initial rapid phenotypic decrease in size would be followed by a more gradual selection and adaption of the genotype to the optimal and smaller size. Lagomorphs are rapidly reproducing herbivores and their smaller size on islands could also be the result of the shortage of the proper kind of food. It is possible that the smaller size of insular carnivores is explained by the same theory and the large *Euarctos a. carlottae*, *Mustela e. haidarum*, and *Martes a. nesophila*, being exceptions to the rule, might be the result of living in the particularly rich food supply of the Queen Charlotte Islands or to the fact that they had adapted to life in the refugia by increasing their body size. The factors influencing the smaller sizes of some insular shrews or the larger sizes of insular marsupials if indeed this trend is general, are not known.

The general trend towards decrease in size on islands of normally large animals could have the same advantage as those who do not put all their eggs into one basket.

As pointed out earlier, the large size of the smaller rodents on islands is probably not attributable to differences in food. It is not known why insular rodents are not smaller, as in many other groups, unless some intrinsic mechanism keeps the populations from depleting the food supply to the point where malnutrition results. One might better consider why mice are usually the size they are on the mainland. They fill a niche as small herbivores and an increase in size could make them more vulnerable to predation in being not only easier to see, but perhaps easier to catch since larger forms are typically more docile (MacArthur 1949, Falconer 1953). Due to the impoverished nature of the insular faunas, the number of predators and competitors would often be greatly reduced thereby making the advantage of being a "normal" size mouse less stringent.

Gene flow may play an important part in limiting the opportunity of a population to adapt to local conditions (Mayr 1954, Ford 1955, Anderson 1960). Where on large islands or on the mainland the animal adapts to the average conditions due to gene flow between the panmictic populations, on small islands the adaptations may be more precise. The slight gene flow to the Chaatl and Tasu populations of Peromyscus from the more variable environment of the interior of the islands could have retarded the progress towards the large size so apparent on the islands to which gene flow would be slight.

Cope (1896) points out that the trend towards larger size is widely spread in the animal kingdom. Indeed, progressively increasing size in lines of descent is one of the most frequent and general phenomenon of orthogenic evolution.

The above discussion presupposes that there is some advantage to a mammal in becoming large if ecological conditions permit. Rensch (1959, p. 210) discusses at length the mechanisms which could confer an advantage on being large: interuterine competition puts a premium on speed of development and large size (the smaller embryos may be absorbed) which continues after birth; they live longer thereby having more time to accumulate antibodies, gather experience, etc.; large size could be important in intraspecific competition; there may be an organizational advantage in having more nerve cells; larger animals are more efficient metabolically, thereby tending to have a longer life.

Hayward (1963) is at present conducting experiments upon the basal metabolic rate of various races of *Peromyscus*, including *keeni* and *prevostensis* and finds that the larger form is metabolically more economical than would be expected from its being larger. This is not because *prevostensis* has a higher percentage of its weight as fat, indeed, it is one of the leanest of the races being considered by Hayward. The difference is likely genetic since the animals have been living on the same diet for two years. Work such as that of Hayward, or Bowman (1961) on the morphological adaptations of Darwin's Finches, could reveal the underlying causes of the trends outlined in this paper.

In addition to the body size, the length of the tail has often been found to be shorter in insular mice. The example of the change in tail length of *prevostensis* on Kunghit Island suggests that a longer tail is important in increasing agility to escape enemies or competitors and when the latter are reduced, the tail length shortens. Other factors could be operative. Ogle (1934) finds that laboratory mice raised in a cold room have tails significantly shorter than the controls raised under normal temperatures, but it is not known whether this has any bearing on the present study. It is possible that the smaller islands have cooler summer temperatures thereby affecting the proportions of the growing mice.

The observation that mice from small islands tend, on the average, to live longer than do those from elsewhere could be accounted for by less successful reproduction on these islands. This is unlikely, however, since the mice, if present on an island, were generally found to be abundant. An explanation in keeping with the general theory holds that the animals are more closely adapted to their environment and thereby the reproductive rate drops and the animals live longer.

The most general trend among the four native carnivores of the Queen Charlotte Islands is towards a heavier preorbital region and/or more massive teeth than is found in their nearby relatives. One would imagine that this phenomenon is somehow caused by differences in the food of these animals peculiar to the islands. While it is known that all the species are most frequently seen near or on the beach and presumably gather much of their food there, this is only a suggestion and perhaps an indication as to where future research to elucidate this problem should lie.

The Charlotte bear is further distinguished by lacking the brown colour phase which is also absent from the species on Vancouver Island and the Alexander Archipelago. The disparity between the sizes of the sexes of the weasel is less on Vancouver Island and the Queen Charlotte Islands. It is impossible at this time to give reasons for these phenomena.

SUMMARY

The Queen Charlotte Islands are the most isolated islands in British Columbia and thereby afford an excellent opportunity to study the evolution of the eight species of native land mammals.

Two summers were spent in collecting mammal specimens on 45 of the islands. The bulk of the specimens examined comprised 825 deer mice (*Peromyscus*) putatively of two species (*maniculatus* and *sitkensis*), and 164 shrews (*Sorex obscurus*) of two races (*elassodon* and *prevostensis*). Specimens from these genera were taken on 29 and 26 islands respectively and contribute most to the study of the insular populations. Forty-two specimens of black bear (*Euarctos americanus carlottae*), 35 marten (*Martes americana nesophila*) and six otter (*Lutra canadensis periclyzomae*) are also examined. No specimens of caribou (*Rangifer dawsoni*) or ermine (*Mustela erminea haidarum*) were taken and the former is presumed to be extinct. Specimens from within and adjacent to the Queen Charlotte Islands were borrowed from other museums to increase the scope of the study. A wide survey of the literature on the characteristics of insular races of mammals was made dealing mostly with the islands in western North America from Panama to the Bering Sea, and some of the islands in Great Britain.

A frequent polemical problem in such studies is to decide whether the differences between the insular races and those of the mainland, or similarities within the insular samples, are attributable to their being of a relict distribution or to the fact that they have evolved their particular characteristics *in situ.* Complete absence of fossil evidence negates the possibility of reaching a firm conclusion. When first proposed, the relict hypothesis best explained the data as known then, but recent indirect evidence suggests that most of the differences in the island forms when compared with mainland relatives are the result of divergent evolution, while the similarities within the samples from the islands are the consequence of parallel evolution.

The strongest evidence in support of these contentions is the uniformity of similarities displayed when a wide selection of island forms are compared with their relatives on the nearby mainland. Artiodactyls, lagomorphs and carnivores tend to be smaller on islands, while many rodents are usually larger, older and with shorter tails. Such a regularity which could be considered as an ecological rule, is not compatible with the relict hypothesis. While the similarities exist, other characteristics are more varied than one would expect if the relicts were formerly members of one population.

The endemic races of Charlotte birds exhibit features characteristic of insular forms from elsewhere in having longer beaks and/or tarsi and are in accord with Gloger's Rule. Apparently they evolved their peculiarities as a consequence of isolation since glaciation.

It has been established that all the native species of mammals of the Queen Charlotte Islands except the caribou could have found the glacial refugia on the Islands suitable for habitation during the last (Vashon) glaciation, thereby allowing at least 100,000 years for the evolution of the characteristics found only in the insular races.

The analysis of the specimens suggests that ancestors to the bear, marten, weasel and one race of shrew (*S. o. elassodon*) existed in the refugia during the last glaciation and evolved their distinctive characteristics therein. The otter, *S. o. prevostensis* and deer mouse do not require such a period in isolation to explain their present form and distribution. It is thought that an average size mouse entered the general region following the retreat of the glaciers and reached most of the islands. These evolved into large mice with usually short tails on the small, isolated, islands where a small, isolated, gene pool permitted them to adapt more precisely to the impoverished environment. The study further indicates that *P. sitkensis* is conspecific with *P. maniculatus* and that *P. m. hylaeus* is consubspecific with *P. m. keeni*. Slight differences are encountered between most of the island samples of small mammals but none are dramatic enough to warrant the description of new forms. Haida Indians undoubtedly played a role in distributing some of the mammals.

Reasons are suggested for the evolution of the insular characteristics and herein lies the most fascinating area for future work.

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APPENDIX

The formula used to calculate whether two eigenvalue plots are significantly different was first developed by Hotelling (1931) and has been given to me by S. W. Nash, Department of Mathematics, University of British Columbia.

The precise test for the difference of any two sample means is:

$$T^2 = \left(\frac{n_h \; n_k}{n_h \; n_k}\right) \overset{m}{\underset{i\,=\,1}{}} \left(z_{ih} - z_{ik}\right)^2$$

where n_h = number in h^{th} group

n_k = number in k^{th} group

m = number of discriminants

z_{ih} = i^{th} discriminant, h^{th} group

z_{ik} = i^{th} discriminant, k^{th} group

If T^2 is greater than $\left(\frac{rm}{r - p\,1}\right)$ F_a the means are significantly different at the *a* level.

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